

## Redescriptions of *Grania americana*, *G. bermudensis* and descriptions of two new species of *Grania* (Annelida: Clitellata: Enchytraeidae) from Bermuda

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*Abstract.*—The diversity of the enchytraeid genus *Grania* is reexamined in Bermuda. Herein, four species, *G. bermudensis* Erséus & Lasserre, 1976, *G. americana* Kennedy, 1966, *G. laxartus*, new species, and *G. hylae*, new species, are described from intertidal and subtidal sand habitats of Bermuda. *Grania americana* and *G. laxartus* are also reported from the Caribbean area and *G. hylae* from Florida. *Grania bermudensis* is recognized as a separate species rather than as a subspecies of *G. macrochaeta* (Pierantoni, 1901). *Grania americana* and *G. laxartus* have distinctive spermathecal structures and the latter has a penial stylet. *Grania bermudensis* and *G. hylae* can be easily separated from their Bermudian congeners by the dorsal position of spermathecal pores. Both *G. americana* and *G. hylae* have statocyst-like sensory structures associated with their brains. These studies provide new information diversity, distribution and taxonomy of *Grania* species of the North Atlantic and on the structural diversity of male duct systems and of statocyst-like sensory structures.

The taxonomic diversity of the abundant and widespread marine oligochaete genus *Grania* Southern, 1913 (Annelida: Clitellata: Enchytraeidae) in Bermuda has been poorly investigated, as have most genera of the marine Enchytraeidae (Healy & Coates 1999). Only one species, *Grania bermudensis* Erséus & Lasserre, 1976, has been described from Bermuda and it was recognized as a subspecies of *G. macrochaeta* (Pierantoni, 1901) (Erséus & Lasserre 1976, Locke & Coates 1998). However, a great degree of anatomical variability among *Grania* specimens collected from Bermuda has been recognized for some time (Erséus, pers. comm.). Furthermore, there are only four publications referring primarily to the Enchytraeidae of Bermuda (Moore 1902, Lasserre & Erséus 1976, Giere 1979, Healy & Coates 1999) and the most recent of these shows the species diversity of this

family is much higher than previous studies indicated.

The single species of *Grania* described from Bermuda was reported prior to the recognition of a variety of important taxonomic characters for this genus. Coates (1984) provided new criteria for categorizing forms of the male duct system found in the genus. These characteristics have played a significant role in the distinction of several new species (e.g., Coates & Erséus 1985, Erséus 1990a, Coates & Stacey 1993). Recently, another interesting structural character was revealed by Rota & Erséus (1996). In a few new species from the Antarctic and Subantarctic, a structure was observed which they called the head organ (Rota & Erséus 1996, 1997). It was described as a vesicular body with refractile inclusions, located within the peristomium just anterior to the brain. Such advances in recognition of morphological characters

have resulted in increased knowledge of specific diversity and provide additional clues that can be applied to discovering evolutionary relationships among species of *Grania* (Locke 1999a).

Observations of type specimens of *G. bermudensis* revealed undescribed, diagnostic characteristics of the spermathecae of this species. These observations, combined with additional information about the form of the male ducts (Coates 1984), suggested that *G. bermudensis* was in need of redescription.

A major marine faunal element in Bermuda is species with Caribbean and coastal southern U.S. distributions (Fig. 1) (Sterrer 1986, 1998). *Grania americana* is the only described species of *Grania* with such a distribution. This species was first reported from the shores of Florida and Bimini (Kennedy 1966) and there have been no subsequent records. In the most recent taxonomic discussion of this species, Erséus & Lasserre (1976) stated that *G. americana* must be considered a nomen dubium due to the poor condition of the type material and lack of detail in the original description. They also suggested it probably was very similar to *G. bermudensis*, implying that *G. americana* might also be a subspecies of *G. macrochaeta*. In fact, Lasserre (1967) had designated *G. americana* as a subspecies of *G. macrochaeta* along with many other species of *Grania*. The basis for this designation, as discussed by Locke & Coates (1998, also see Locke 1999a), was probably largely historical and possibly eurocentric. Oligochaetes have long been considered a lineage that originated and diversified in non-marine habitats and, thus, a low species diversity in marine systems was expected. In contrast to the early opinion of Lasserre (1967), Erséus (1974) had noted *G. americana* and *G. macrochaeta* were probably separate species based on definite and consistent morphological differences, but that additional information about intraspecific variation of each taxon was needed.

New taxonomic characteristics and com-

plete redescriptions are presented to substantiate the morphological differences among *G. americana*, *G. bermudensis* and *G. macrochaeta* sensu stricto. Redescriptions of the first two taxa and a survey of *Grania* species in Bermuda were undertaken in order to advance understanding of the diversity, zoogeography and evolution of marine oligochaetes.

## Materials and Methods

Sediments were collected from three intertidal sites and nine subtidal sites within Bermuda. Intertidal sites were Ferry Point Bridge, Whalebone Bay and Rocky Hill Park, where samples were taken from an accumulation of sand inside dissolution tubes in limestone rock and from two rocky limestone beach areas, respectively. Subtidal sites were from Castle Harbour: Eastern Castle Roads, Rushy Island, and a patch reef 100 m from Rushy Island; St. George's Harbour: ENE and SE Paget Island; Ferry Reach; NW Pearl Island in Great Sound; NE entrance of Smith's Sound; and Bailey's Bay. Other specimens were provided by C. Erséus, from Hutchinson Island, Florida; Fowey Rocks, Miami, Florida; North of Angelfish Key, Florida Keys; and Carrie Bow Cay, Belize (Table 1).

Specimens collected by the authors in Bermuda were obtained by washing samples on a 300  $\mu\text{m}$  sieve and then sorting the residue in seawater using a dissecting microscope. Specimens were fixed in Kahle's fluid, stained lightly with borax carmine, dehydrated and cleared, and mounted in Canada balsam for morphological observations. Only mature specimens were identified. Specimens of all *Grania* species found in Bermuda were also observed while alive.

Type specimens of *G. americana* (USNM 33005) and *G. bermudensis* (USNM 53202), Castle Island, were borrowed from the United States National Museum of Natural History (USNM) (Smithsonian Institution), Washington, D.C., and

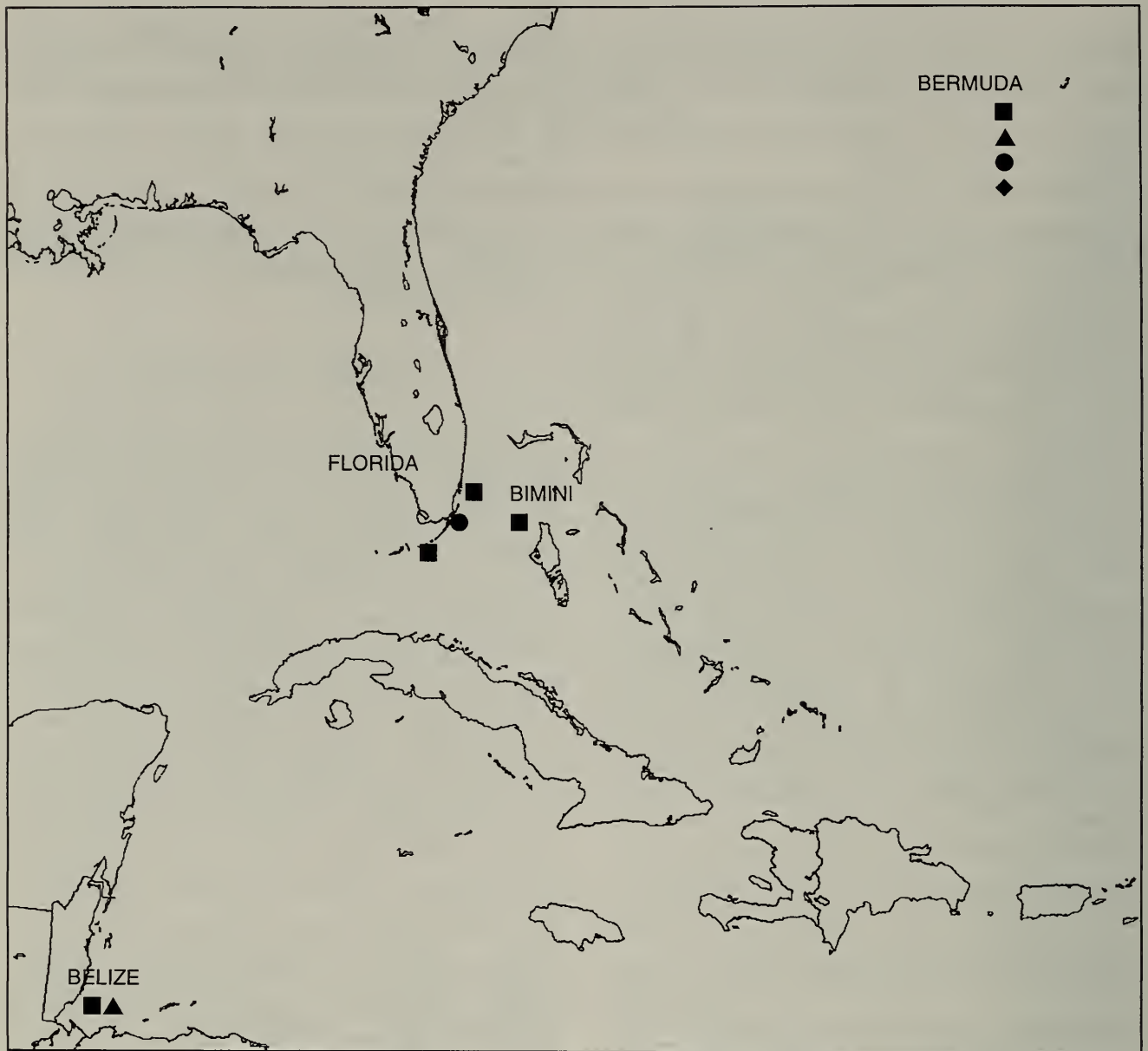


Fig. 1. Distribution of *Grania* species found in Bermuda in coastal North American, Bermudian and Caribbean waters. ■ *G. americana*, ▲ *G. laxartus*, ● *G. hylae*, ◆ *G. bermudensis*.

examined for identification of and comparison with the new specimens. Whole mounted specimens of *Grania monospermatheca* Erséus & Lasserre, 1976, *G. americana*, *G. bermudensis*, and *Grania atlantica* Coates & Erséus, 1985, and the new species described herein were also examined from the collections of the authors (KAC) and C. Erséus.

Observations of specimens were made using differential interference contrast light microscopy and videomicroscopy. Thirty-five mm photography was done with a Wild MPS46 photoautomat on Kodak Technical Pan film ASA 100. Drawings were made

with the aid of a drawing tube. An Olympus AX70 Provis microscope and Toshiba 3CCD camera with Image-Pro Plus™ software were utilized for video microscope image capture analysis and morphological measurements. Measurements were also taken with the use of Jandel Video Analysis Software (JAVA) and with the aid of an ocular micrometer. The mean ( $\bar{X}$ ) and standard deviation (*SD*) were calculated for morphometric data.

Measurements for *G. americana* and one new species were made from Bermuda and Carrie Bow Cay whole mounted specimens; for the other new species and *G. bermu-*

Table 1.—Site location and substrate description. For more complete Carrie Bow Cay data, refer to Erséus (1990b).

Site	Date	Position	Depth	Description	Species
<b>Bermuda</b>					
Whalebone Bay	Dec 1977	32°21'90"N 64°42'75"W	intertidal	fine to coarse	<i>G. laxartus</i> , <i>G. americana</i>
Ferry Point Bridge	1996–1998	32°21'70"N 64°42'80"W	intertidal	dissolution tubes	<i>G. laxartus</i> , <i>G. americana</i>
Rocky Hill Park	Oct 1998	32°22'60"N 64°41'40"W	intertidal	coarse with rocks	<i>G. hylae</i> , <i>G. americana</i>
Pearl Island	Aug 1977	32°17'50"N 64°50'19"W	2.5 m	fine	<i>G. laxartus</i> , <i>G. americana</i>
Ferry Reach 1	Nov 1977	32°22'05"N 64°41'44"W	0.2 m	medium to coarse	<i>G. laxartus</i> , <i>G. americana</i>
Ferry Reach 2	Dec 1977	32°22'05"N 64°41'44"W	0.5 m	medium to coarse	<i>G. laxartus</i>
NW Smith's Snd	Dec 1977	32°22'14"N 64°39'21"W	4 m	fine with seagrass	<i>G. laxartus</i>
Castle Island	Aug 1977	32°20'40"N 64°40'25"W	15 m	medium to coarse	<i>G. hylae</i> , <i>G. bermudensis</i>
Bailey's bay	Aug 1977	32°20'94"N 64°43'30"W	6.5 m	fine to medium	<i>G. hylae</i> , <i>G. americana</i>
ENE Paget Island	Dec 1977	32°22'38"N 64°38'57"W	17 m	medium to coarse	<i>G. hylae</i>
SE Paget Island	Dec 1977 & Mar 1998	32°22'35"N 64°39'30"W	8 m, 15 m	medium to coarse	<i>G. hylae</i> , <i>G. bermudensis</i>
E Castle Roads	Aug 1977	32°20'30"N 64°40'20"W	8 m	coarse	<i>G. bermudensis</i>
Rushy Island	Aug 1977	32°20'18"N 64°40'45"W	8–9 m	coarse	<i>G. bermudensis</i>
Patch Reef	Aug 1977	32°20'19"N 64°40'26"W	8–9 m	coarse	<i>G. bermudensis</i>
<b>Florida</b>					
Fowey Rocks	Nov 1977	25°35.5'N 80°05.8'W	3 m	coarse	<i>G. hylae</i>
N. Angelfish Key	Nov 1977	25°10'N 80°13'02"W	6 m	<i>Thalassia</i> , fine	<i>G. americana</i>
Hutchinson Island	Nov 1972/May 1973	27°20'24"N 80°13'04"W	10 m	shell rubble	<i>G. americana</i>
<b>Carrie Bow Cay, Belize</b>					
cbc-85-2	Nov 1985	all stations	all stations	medium to coarse	<i>G. laxartus</i> , <i>G. americana</i>
cbc-85-2-14	Nov 1985	16°48'N	1.5 m	medium to coarse	<i>G. americana</i>
cbc-85-15	Nov 1985		0.5 m	medium to coarse	<i>G. americana</i>
cbc-85-26	Nov 1985		0.2 m	<i>Thalassia</i> , rubble	<i>G. americana</i>
cbc-85-36	Nov 1985		1 m	muddy	<i>G. laxartus</i>
cbc-85-41	Nov 1985		0.2 m	grey, coarse	<i>G. americana</i>
cbc-85-57	Nov 1985		1 m	medium to coarse	<i>G. laxartus</i>
cbc-85-65	Nov 1985		1 m	medium to coarse	<i>G. americana</i>
cbc-85-68	Nov 1985		0.1 m	<i>Thalassia</i> , coarse	<i>G. laxartus</i>
			0.3 m	coarse, rubble	<i>G. americana</i>

*densis*, measurements were taken from whole mounts of Bermuda specimens. Terminology for the head organ was adapted from Rota and Erséus (1996, 1997) and for penial bulb types from Coates (1984). Observations of the "head organ" indicate that a more appropriate name for this structure would be the anterior brain vesicle.

### *Grania* Southern, 1913

For a recent synonymy of the genus refer to Locke & Coates 1998.

#### *Grania laxartus* new species

Figs. 2–6; Table 1

*Holotype*.—USNM 185951, stained, whole mounted specimen, collected Feb. 1996 by KAC.

*Type locality*.—Ferry Point Bridge, Bermuda. 32°21'70"N, 64°42'80"W. Intertidal coarse biogenic sands within dissolution tubes.

*Paratypes*.—Three whole mounted specimens, USNM 185952 Ferry Reach, Bermuda, BBS-77-38, C. Erséus 1977; USNM 185953 Carrie Bow Cay, Belize, CBC 85-41, C. Erséus 1985; and Bermuda Aquarium, Museum and Zoo, BAMZ 1999 180 006 Ferry Reach, Bermuda, BBS-77-41, C. Erséus 1977.

*Other material examined*.—About 45 live specimens from the type locality collected by the authors over the period 1996–1998. Twenty-six whole mounts from type locality, collected (KAC) February and March, 1996. Fourteen whole mounts collected by C. Erséus from Bermuda. Five whole mounts collected from Carrie Bow Cay, Belize, by C. Erséus (Table 1).

*Description*.—External characteristics: Live specimens translucent white with a pink tinge due to colored blood within their vessels. Preserved length 4.7–8.3 mm ( $n = 18$ ,  $\bar{X} = 6.7$ ,  $SD = 1.1$ ). Number of segments 33–64 ( $n = 20$ ,  $\bar{X} = 50.0$ ,  $SD = 9.3$ ). Diameter at 4/5 90.0–160.0  $\mu\text{m}$  ( $n = 29$ ,  $\bar{X} = 129.4$ ,  $SD = 15.9$ ), diameter at clitellum 100.0–198.2  $\mu\text{m}$  ( $n = 26$ ,  $\bar{X} = 138.0$ ,  $SD$

$= 18.3$ ) (Fig. 2). Head pore located in anterior region of peristomium. Setae (Figs. 2 & 3) present from IV ventrally and XVI–XVIII laterally; setae absent in XII of mature worms. Ventral setae anterior to the clitellum appear more robust and thicker than postclitellar setae. Setae are pointed distally and somewhat broad at base and with a curve and slight toe at the proximal end but no distinct heel (Fig. 3). Length of anterior ventral setae 38.0–56.0  $\mu\text{m}$  ( $n = 16$ ,  $\bar{X} = 48.4$ ,  $SD = 5.1$ ); midbody ventral setae 34.0–50.0  $\mu\text{m}$  long ( $n = 28$ ,  $\bar{X} = 42.0$ ,  $SD = 4.35$ ); postclitellar lateral setae 38.0–48.0  $\mu\text{m}$  long ( $n = 18$ ,  $\bar{X} = 42.4$ ,  $SD = 2.8$ ). In ten posterior-most segments ventral setae ranged from 37.3–75.5  $\mu\text{m}$  ( $n = 9$ ,  $\bar{X} = 45.7$ ,  $SD = 11.7$ ) and lateral setae from 36.0–45.2  $\mu\text{m}$  in length ( $n = 11$ ,  $\bar{X} = 42.5$ ,  $SD = 3.2$ ). Spermathecal pores paired, lateral, immediately posterior to 4/5. Clitellum extends from mid XI to mid XIII. Male pores ventral, in line with ventral setae of preceding segments, located at about midpoint of XII. Female pores more lateral than male pores, just posterior to 12/13.

Internal somatic characteristics: Brain narrow anteriorly and indented posteriorly. No anterior brain vesicle. Ventrolateral pharyngeal gland lobes very small in IV. Small dorsolateral lobes at 4/5; two pair of small ventrolateral lobes in V and one dorsolateral pair at 5/6; in VI, two or three pairs of ventrolateral lobes and one lateral pair at 6/7 (Fig. 2). Coelomocytes numerous anteriorly, not found posterior to clitellum. Patterned chloragogen cells covering posterior regions of the intestine, which often contains pennate diatoms. Nephridia not seen. Dorsal blood vessel transition to blood sinus in XXVI. No glands on ventral nerve cord.

Internal reproductive characteristics: Spermathecae (Fig. 4) paired in anterior of V, ampulla with narrow, ventrolateral, ental connection to esophagus; connection more ventral than line of ectal spermathecal pores. Spermathecal ectal duct has large subspherical dilation midway between pore

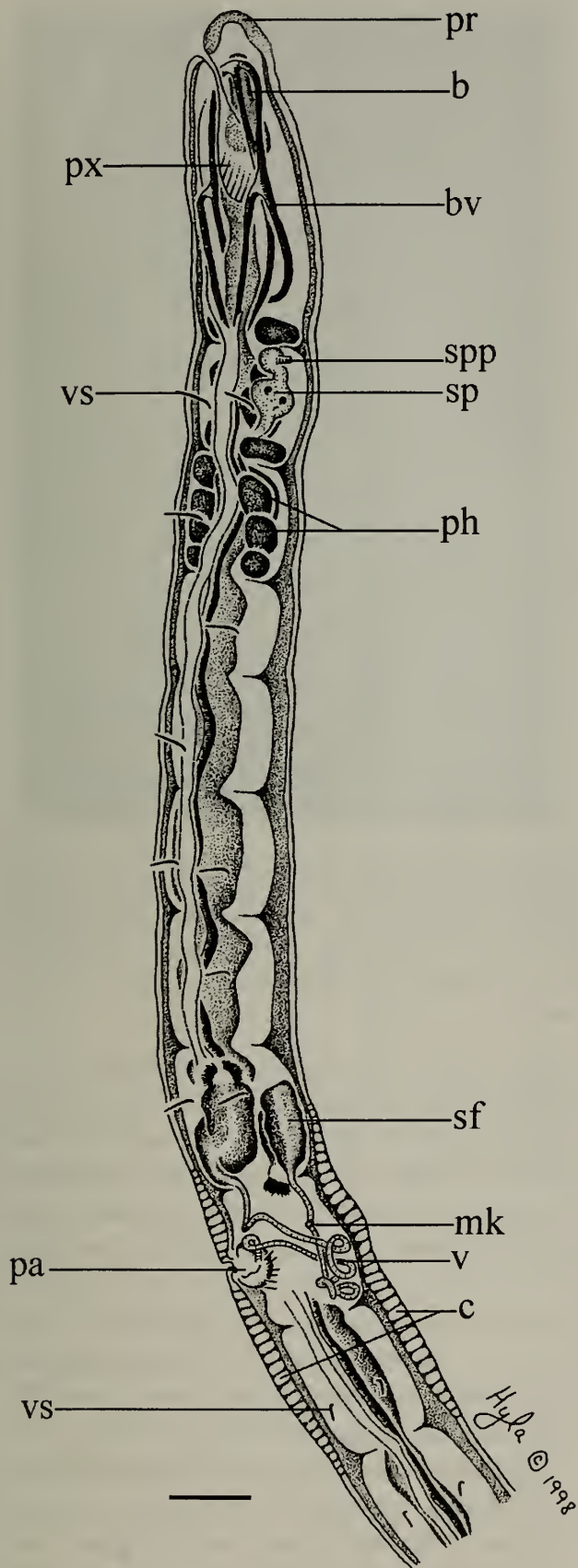


Fig. 2. *Grania laxartus*, new species, specimen from Bermuda. Semischematic ventrolateral view of whole mounted specimen showing only one of the penial apparatuses; prostomium to segment XIV, illustrating position and relative sizes of diagnostic structures. Scale equals 100  $\mu\text{m}$ . b, brain; bv, blood vessel; c, clitellar gland cells; mk, muscle knot on vas defer-

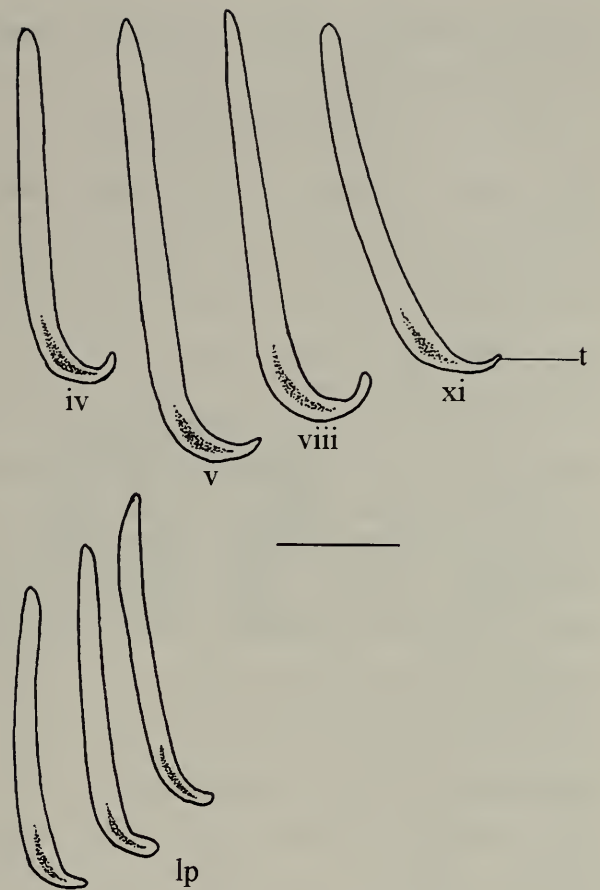


Fig. 3. *Grania laxartus*, new species, from Bermuda. Setae from various positions, showing broad base and slight toe. Scale equals 20  $\mu\text{m}$ . lp, lateral posterior seta, t, setal toe.

and ampulla (Fig. 4). Ectal duct runs at about 90° from body wall to dilation, where it turns 90° to run parallel to body wall. The ectal duct then penetrates the ampulla as a cone-like protrusion (Fig. 4). Diameter of the ectal duct dilation 18.0–32.6  $\mu\text{m}$  ( $n = 54$ ,  $\bar{X} = 25.0$ ,  $SD = 3.0$ ) (Fig. 4). Width of spermathecal ectal duct 10.0–21.9  $\mu\text{m}$  ( $n = 46$ ,  $\bar{X} = 15.5$ ,  $SD = 2.7$ ) between dilation and ampulla and 10.0–14.0  $\mu\text{m}$  ( $n = 31$ ,  $\bar{X} = 11.2$ ,  $SD = 1.5$ ) between dilation and ectal pore. Ampulla roughly spherical, greatest diameter 26.0–50.0  $\mu\text{m}$  ( $n = 54$ ,  $\bar{X} = 42.5$ ,  $SD = 4.7$ ). Rings of sperm in wall of ampulla of reproductive specimens. No

←

ens; pa, penial apparatus; ph, pharyngeal glands; pr, prostomium; px, pharynx; sf, sperm funnel; sp, spermatheca; spp, spermathecal ectal pore; v, vas deferens; vs, ventral seta.

glands at ectal pore (Fig. 4). Sperm funnels 80.0–160.0  $\mu\text{m}$  long ( $n = 25$ ,  $\bar{X} = 112$ ,  $SD = 23.5$ ), 25–55  $\mu\text{m}$  maximum width ( $n = 25$ ,  $\bar{X} = 41.4$ ,  $SD = 9.2$ ) or, length about three times width; attached sperm with straight heads (acrosome & nucleus) (Fig. 5A). Laterally paired vasa deferentia possess a muscular “knot” at one quarter their total length, near sperm funnel (Fig. 5A); muscle bands run around vas and constrict it, but there are no obvious longitudinal extensions of the muscle bands. Vas confined to XI–XIII. Width of vas 6.3–8.8  $\mu\text{m}$  ( $n = 26$ ,  $\bar{X} = 7.6$ ,  $SD = 0.8$ ) both before and after “knot”. Penial apparatus with small gland and lateral aglandular sac formed by extended invagination of male pore, muscles extend from body wall to outer wall of sac (Fig. 5A, B). Vas enters gland from a dorsolateral position, extends through glandular material to medial side. Penial stylet present, walls of vas deferens thin, with pronounced nuclei where stylet begins. Stylet extends from ectal end of vas deferens, tapering toward blind end of sac-like extended invagination of male pore. Length of stylet 30.0–47.7  $\mu\text{m}$  ( $n = 12$ ,  $\bar{X} = 33.9$ ,  $SD = 6.5$ ); maximum width of stylet 1.7  $\mu\text{m}$  (measured for only two specimens) (Fig. 5B). Posterior extension of sperm sac XVIII through XXI. Egg sac extends to XXIII, with primary oocytes located only at posterior end of sac.

*Etymology.*—The species is named in allusion to the unique shape of the spermathecal ectal duct; *laxartus* from the Latin *laxus* meaning wide or broad, combined with *artus* meaning joints; a noun in apposition.

*Taxonomic remarks.*—Lateral setae are reported as commencing in XVI–XVIII, however, one specimen was an exception with lateral setae beginning in XXV and with ventral setae lacking from XVIII–XXIII. The ventral setal distribution for *G. laxartus* is similar to *G. bermudensis*, *G. americana* and *G. hylae* (Fig. 6) from the Northwest Atlantic. The last three species are easily distinguished from *G. laxartus* by

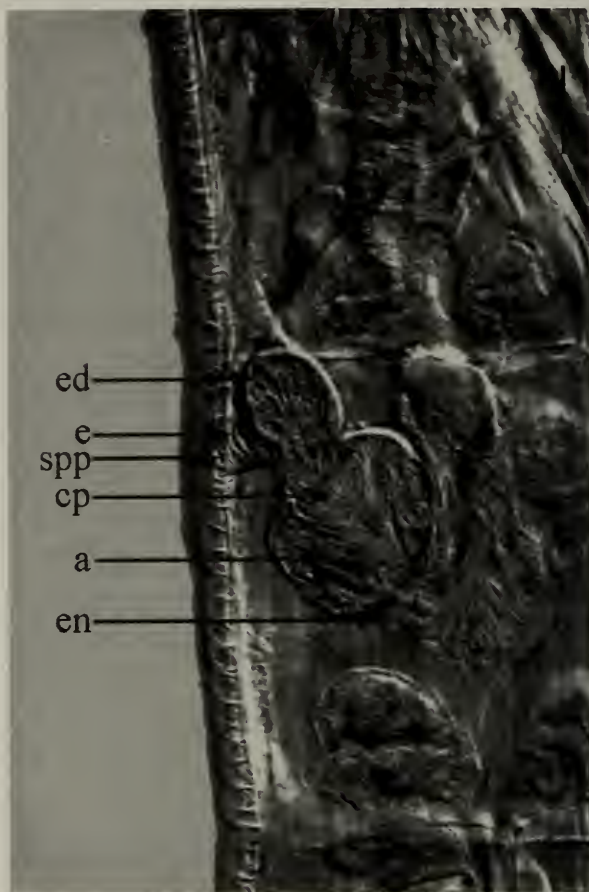


Fig. 4. *Grania laxartus*, new species, from Bermuda. Dorsal view of spermatheca in V. Scale equals 20  $\mu\text{m}$ . a, ampulla; cp, conical protrusion of spermathecal duct; e, spermathecal ectal duct; ed, ectal dilation; en, spermathecal ental duct; see Fig. 2 for other symbols.

dorsal spermathecal pores and a muscular sac-like penial apparatus in both *G. bermudensis* and *G. hylae*, and by the absence of both a penial stylet and muscular vas deferens (Coates 1984) in *G. americana*. Furthermore, *G. bermudensis*, *G. hylae* and *G. americana* each have very different spermathecal morphologies, lacking the distinct dilation of the spermathecal ectal duct that is present in *G. laxartus* (Fig. 6).

This form of dilation of the spermathecal ectal duct is reported in one other species of *Grania* from the Northwest Atlantic, *G. monospermatheca*, and is not known in any other species of *Grania* (Locke & Coates 1998; Rota & Erséus 1996, 1997; Coates & Stacey 1993, 1997; Coates 1990; Erséus 1990a; Coates & Erséus 1985; Coates & Erséus 1980; Erséus & Lasserre 1976). The ectal duct dilation of *G. monospermatheca*

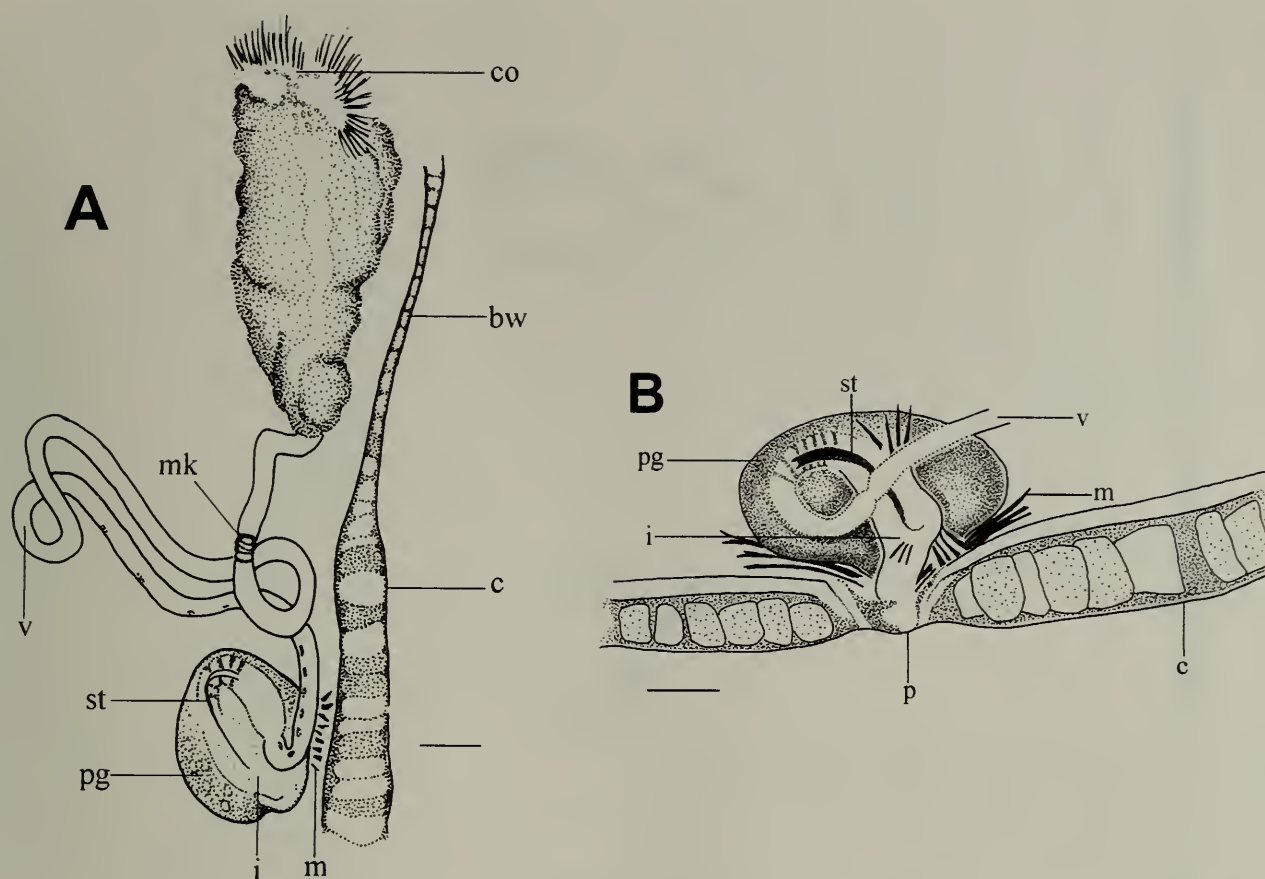


Fig. 5. *Grania laxartus*, new species, from Bermuda. A, ventral view of male duct system showing sperm funnel, vas deferens and penial apparatus. B, lateral view of penial apparatus. Scales equal 20  $\mu\text{m}$ . bw, body wall; co, sperm funnel collar; i, invagination at male pore; m, muscle; p, male pore; pg, penial gland; st, stylet; see Fig. 2 for other symbols.

occurs immediately before the ampulla and is not as distinctly bulb-like as the medial dilation of the spermathecal ectal duct in *G. laxartus*. *Grania monospermatheca* is also readily distinguished from *G. laxartus* by the absence of lateral setae and the presence of a single spermatheca with a dorsal pore instead of a pair of spermathecae which open laterally.

**Habitat and distribution.**—Intertidal pools with accumulations of sand, in dissolution tubes formed by the erosion of limestone rock. Also occurs subtidally. Found in sand samples with debris along with *G. americana* and various Tubificidae, Nematoda and Sipunculida. Sand particle size for samples ranged from fine (occurring with *Thalassia testudinum* Koenig) to medium coarse calcareous coral sand. Known from Ferry Point Bridge, Whalebone Bay, Pearl Island, Ferry Reach and

Smith's Sound, Bermuda; and Carrie Bow Cay, Belize (Table 1).

#### *Grania hylae* new species

Figs. 6, 7–11; Table 1

**Holotype.**—USNM 185954, stained, whole mounted specimen, BBS-77-42, collected by C. Erséus 1977.

**Type locality.**—ENE of Paget Island, Bermuda, 32°22'38"N, 64°38'57"W. Subtidal in 17 m, medium to coarse coral sand.

**Paratypes.**—Three stained, whole mounted specimens, USNM 185955 M77-6, North of lighthouse, Fowey Rocks USA, C. Erséus 1977; USNM 185956 BBS-77-15 Castle Island, Bermuda, C. Erséus 1977; and BAMZ 1999 180 007 BBS-77-15 Castle Island, Bermuda, C. Erséus 1977.

**Other material examined.**—Live material from Rocky Hill Park, Bermuda. Fourteen





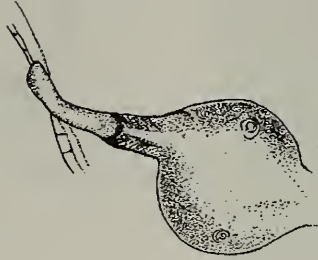

	<i>Grania laxartus</i>	<i>Grania hylae</i>	<i>Grania bermudensis</i>	<i>Grania americana</i>
Length (mm)	6.7	8	7.8	10.8
Number of segments	50	52	51	64
Diameter 4/5 (µm)	129.4	155.9	180.7	168.7
Setal origins ventral lateral	IV XVI-XVIII	IV XV-XVII	IV XVI-XX	IV XVI-XX
Spermathecal pores	lateral	dorsal	dorsal	lateral
Spermathecal shape				
Glands at spermathecal pore	no	no	no	yes
Glands on nerve cord	no	yes	yes	yes
Head organ	no	yes	no	yes
Sperm funnel	L3XW	L2.5XW	L4XW	L8XW
Vas deferens muscular	yes knot	yes thin with constrictions	yes spiral and thick	no
Penial apparatus type (Coates 1984)	5	6	6	3

Fig. 6. Comparison of *Grania* species. Measurements are shown as averages. Spermathecae of *G. bermudensis* and *G. americana* are shown at one-half the magnification used for *G. hylae* and *G. laxartus*.

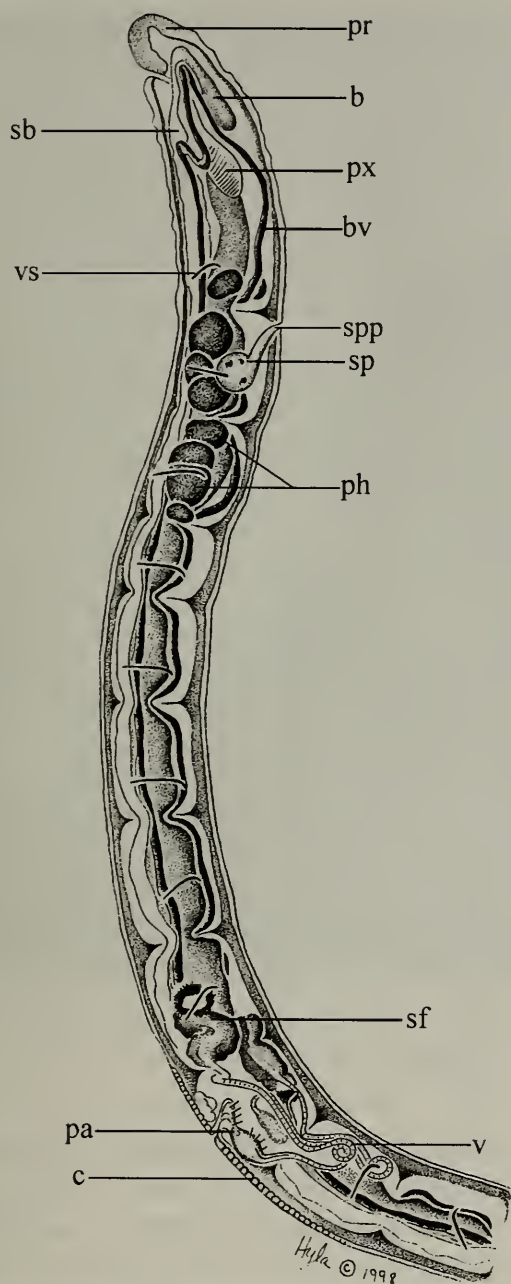


Fig. 7. *Grania hylae*, new species, specimen from Bermuda. Semischematic lateral view of whole mounted specimen; prostomium to segment XIV. Scale equals 100  $\mu\text{m}$ . sb, subesophageal ganglion; see Fig. 2 for other symbols.

whole mounted specimens from the collection of C. Erséus, from three different localities in Bermuda, and Fowey Rocks, Florida, U.S.A. (Table 1).

**Description.**—External characteristics: Fixed specimen length 5.3–11.5 mm ( $n = 7$ ,  $\bar{X} = 8.0$ ,  $SD = 2.1$ ). Number of segments 41–61 ( $n = 6$ ,  $\bar{X} = 52$ ,  $SD = 8.1$ ). Diameter at 4/5 139.5–192.0  $\mu\text{m}$  ( $n = 7$ ,  $\bar{X} = 155.9$ ,  $SD = 17.3$ ), diameter at clitellum 154.0–196.0  $\mu\text{m}$  ( $n = 7$ ,  $\bar{X} = 171.4$ ,  $SD = 17.3$ )

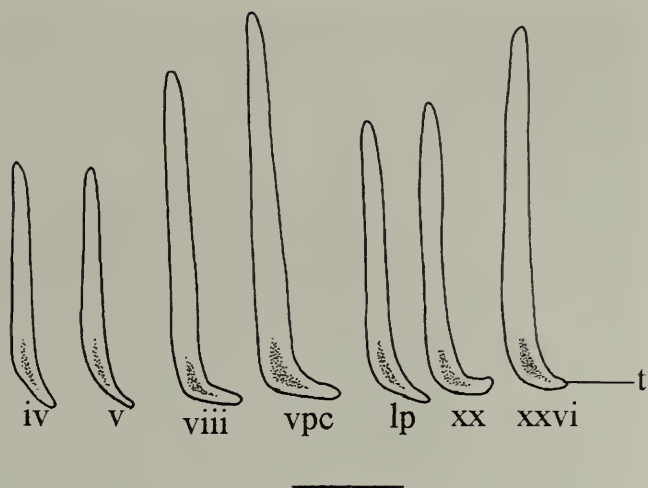


Fig. 8. *Grania hylae*, new species, from Bermuda. Setae from different segments. Scale equals 20  $\mu\text{m}$ . vpc, ventral postclitellar seta; see Fig. 3 for other symbols.

(Fig. 7). Head pore in anterior of peristomium. Ventral setae (Figs. 7 & 8) present from IV and laterally from XV–XVII. No setae in XII of mature specimens. Length of anterior ventral setae 37.0–66.4  $\mu\text{m}$  ( $n = 10$ ,  $\bar{X} = 51.3$ ,  $SD = 8.9$ ); midbody ventral setae 49.8–91.0  $\mu\text{m}$  ( $n = 35$ ,  $\bar{X} = 71.8$ ,  $SD = 8.5$ ); postclitellar lateral setae 59.8–80.0  $\mu\text{m}$  long ( $n = 31$ ,  $\bar{X} = 69.6$ ,  $SD = 5.8$ ). In ten posterior-most segments ventral setae 53.7–71.0  $\mu\text{m}$  ( $n = 17$ ,  $\bar{X} = 62.8$ ,  $SD = 5.2$ ) and lateral setae 49.0–74.0  $\mu\text{m}$  ( $n = 14$ ,  $\bar{X} = 62.2$ ,  $SD = 8.4$ ). Setal shaft widening proximally, with sloping toe, distinct heel absent (Fig. 8). Spermathecal pores paired, dorsal, immediately posterior to 4/5 (Fig. 7), distance between pores 46.0–37.5  $\mu\text{m}$  ( $n = 2$ ,  $\bar{X} = 41.8$ ,  $SD = 6.0$ ), no epidermal papilla at pore. Clitellum extending from post XI to mid XIII. Male pores ventral, in line of setae, at midpoint of XII. Female pores posterior to 12/13, opening just lateral to position of male pores.

Internal somatic characteristics: Brain indented posteriorly with narrow transition to small anterior brain vesicle. Membrane-bound, anterior, brain vesicle lies below head pore, with one refractile inclusion (Fig. 9). Pharyngeal glands present in segments IV through VI; one ventrolateral pair of lobes in IV and one dorsolateral pair at

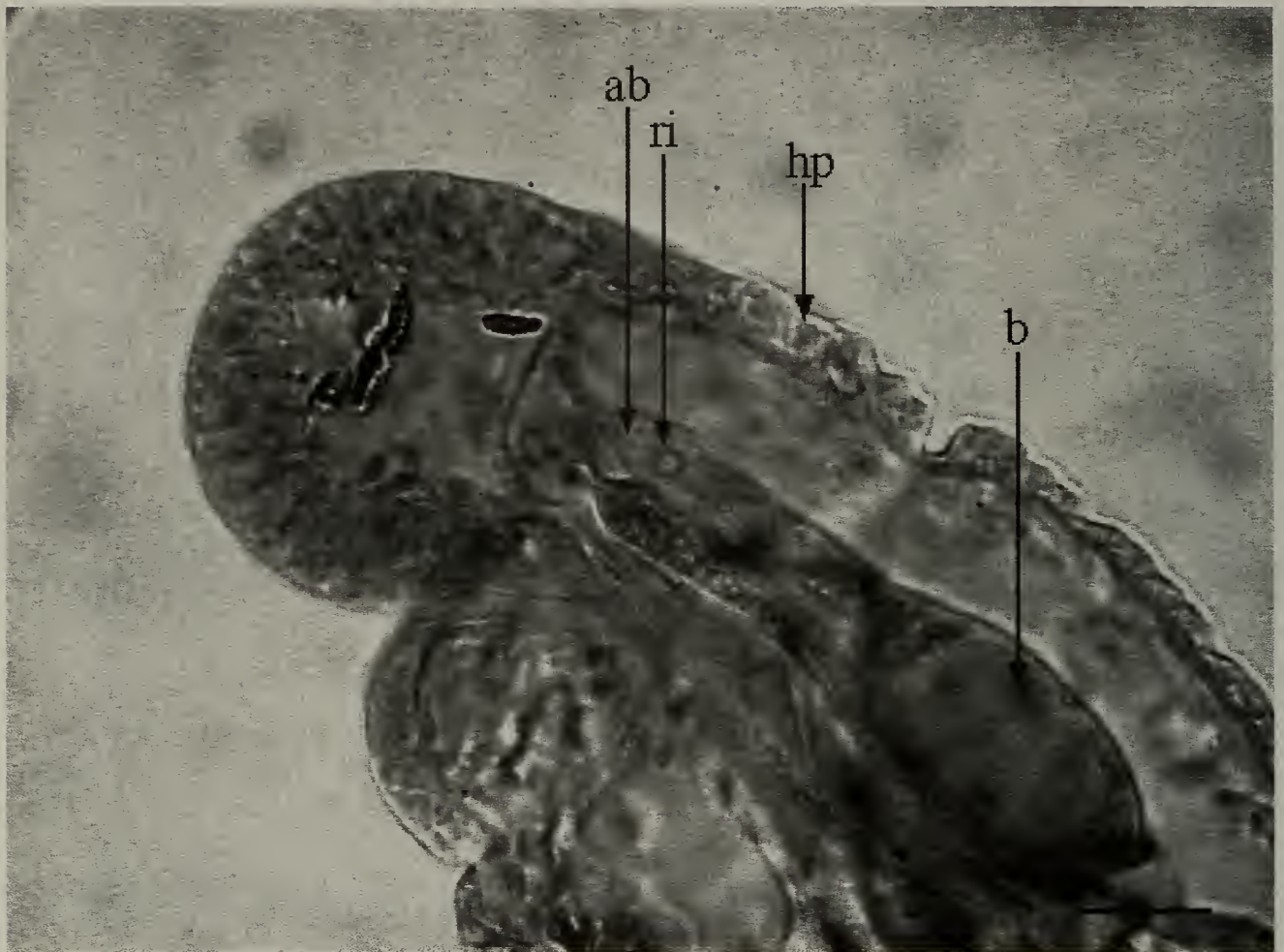


Fig. 9. *Grania hylae*, new species, from Bermuda. Lateral view of anterior brain vesicle with one inclusion. Scale equals 20  $\mu\text{m}$ . ab, anterior brain vesicle; hp, head pore; ri, refractile inclusion; see Fig. 2 for other symbols.

4/5, two paired ventrolateral lobes in V and one dorsolateral pair at 5/6; three pairs of ventrolateral lobes in VI and one dorsal pair at 6/7. No nephridia observed. Dorsal blood vessel transition to blood sinus at XX or XXI. Gland on ventral nerve cord in XIV.

Internal reproductive characteristics: Spermathecae lie dorsal to pharyngeal glands in segment V (Figs. 7 & 10). Spermathecal ectal duct of uniform, narrow width with slight curvature toward pore, length of duct about 1.2 times maximum diameter of ampulla. Glands lacking at ectal pore. No protrusion of duct tissue into ampulla. Spermathecal ampulla small and round to ovoid, maximum diameter 32.0–52.0  $\mu\text{m}$  ( $n = 11$ ,  $\bar{X} = 43.8$ ,  $SD = 6.3$ ); ampullae lie close together, dorsal to gut, sometimes even touching; sperm rings present (Fig. 10). Narrow ental connection of spermathecal ampulla to esophagus. Sperm

funnel length two and a half times the width, with non-granular section posterior to collar. Vasa deferentia confined to XII and XIII. Wall of vas deferens constricted at three almost equally spaced points immediately posterior to union with sperm funnel; with slight muscularization ectal to constrictions (Fig. 11A); vas possesses large, obvious nuclei along length, diameter of vas uniform along length 6.7–10.0  $\mu\text{m}$  ( $n = 13$ ,  $\bar{X} = 8.4$ ,  $SD = 0.9$ ). Penial apparatus bipartite, with horizontal and erect sections. Penial stylet present, originating within the vas deferens, extending just into the penial apparatus (Fig. 11A, B). Stylet long, 55.4–70.9  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 61.8$ ,  $SD = 7.1$ ). Vas terminates at ental end of the saccate part of the bipartite penial apparatus, which lies parallel to body wall and gut. This sac may appear longitudinally ridged or smooth, depending on whether it

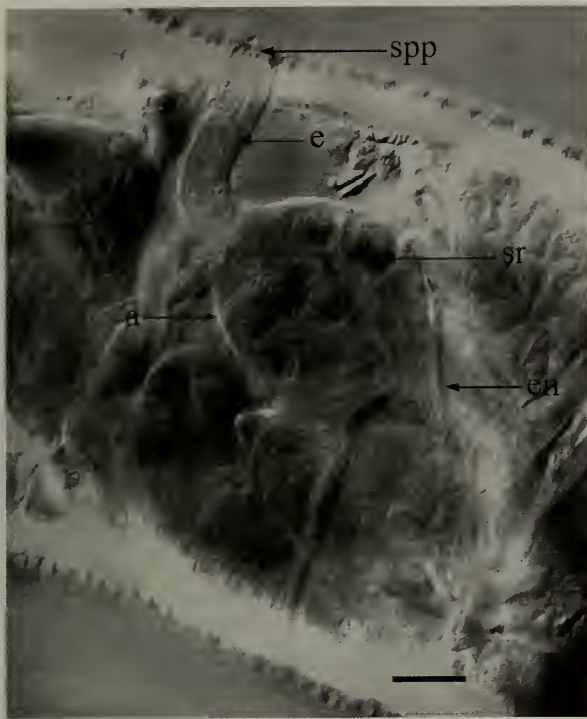


Fig. 10. *Grania hylae*, new species, from Bermuda. Lateral view of spermatheca in V, with dorsal pore. Scale equals 20  $\mu\text{m}$ . sr, sperm ring; see Fig. 4 for other symbols.

is contracted or relaxed. At anterior end of sac, there is an acute to right angle bend that unites the ridged, contracted sac to an erect extension of the male pore (standing more or less perpendicular to the body wall). Muscles run from the body wall to insert on both the longitudinal sac and onto the lateral wall of the perpendicular extension (Fig. 11A, B). Sperm sac extends to XVIII. Egg sac extends to XXII.

*Etymology*.—Named *hylae* in appreciation of Hyla Tibbitts' dedication and keen interest in the subject matter of her illustrations.

*Taxonomic remarks*.—*Grania hylae* has similarities to *G. bermudensis* in subtidal habitat, although it has also been found in the lower intertidal of rocky beaches, and in the structure of both spermathecae and the penial apparatus. Both species have dorsal spermathecal pores and round to ovoid ampullae. The average maximum diameter of the spermathecal ampulla for *G. hylae*, however, is only half that for *G. bermudensis*. An epidermal bump at the ectal pore is also seen only in *G. bermudensis* as well as a widening of the ectal duct near the ampulla.

*Grania hylae* possesses an anterior brain vesicle which is lacking in *G. bermudensis*. Differences between the two species are also seen in the details of the male duct systems. The walls of the vas deferens in *G. bermudensis* are highly muscularized whereas those of *G. hylae* have only a thin muscle layer. The maximum width of the muscular part of the vas deferens in *G. bermudensis* averages 22.9  $\mu\text{m}$  and the non-muscular sections 12.3  $\mu\text{m}$ ; *G. hylae* has an average vas width of 8.4  $\mu\text{m}$ . Both species do possess bipartite penial apparatuses with longitudinal sac-like parts but the junctions of vas deferens and penial sac are quite different.

There are a few other species of *Grania* which also have dorsally positioned spermathecal pores, including *Grania maricola* Southern, 1913 (see also Locke & Coates 1998) in which the pores are distinctly dorsal to the midlateral line although not fully dorsal. Both *Grania inermis* Erséus, 1990 and *Grania stilifera* Erséus, 1990 described from around Hong Kong (Erséus 1990a) have dorsal spermathecal pores but the first of these does not have a penial stylet and the second is reported to have a large gland associated with the penial apparatus. There are no separate glands on the penial apparatus of either of the species with dorsal spermathecal pores which are found in Bermuda, *G. hylae* and *G. bermudensis* (see below).

*Habitat and distribution*.—Subtidal, found in fine, medium and coarse coral sand, many Tubificidae also present. Intertidal, rocky limestone beach area, medium to coarse sand, with *G. americana*, Tubificidae and Nematoda. Known from Rocky Hill Park, Castle Island, Bailey's Bay, and ENE and SE Paget Island, Bermuda; and Fowey Rocks, Miami, Florida, U.S.A. (Table 1).

*Grania bermudensis* Erséus & Lasserre, 1976

Figs. 6, 12–15; Table 1

*Grania macrochaeta bermudensis* Erséus & Lasserre, 1976:122–124, fig. 3; Lasserre & Erséus 1976:453.

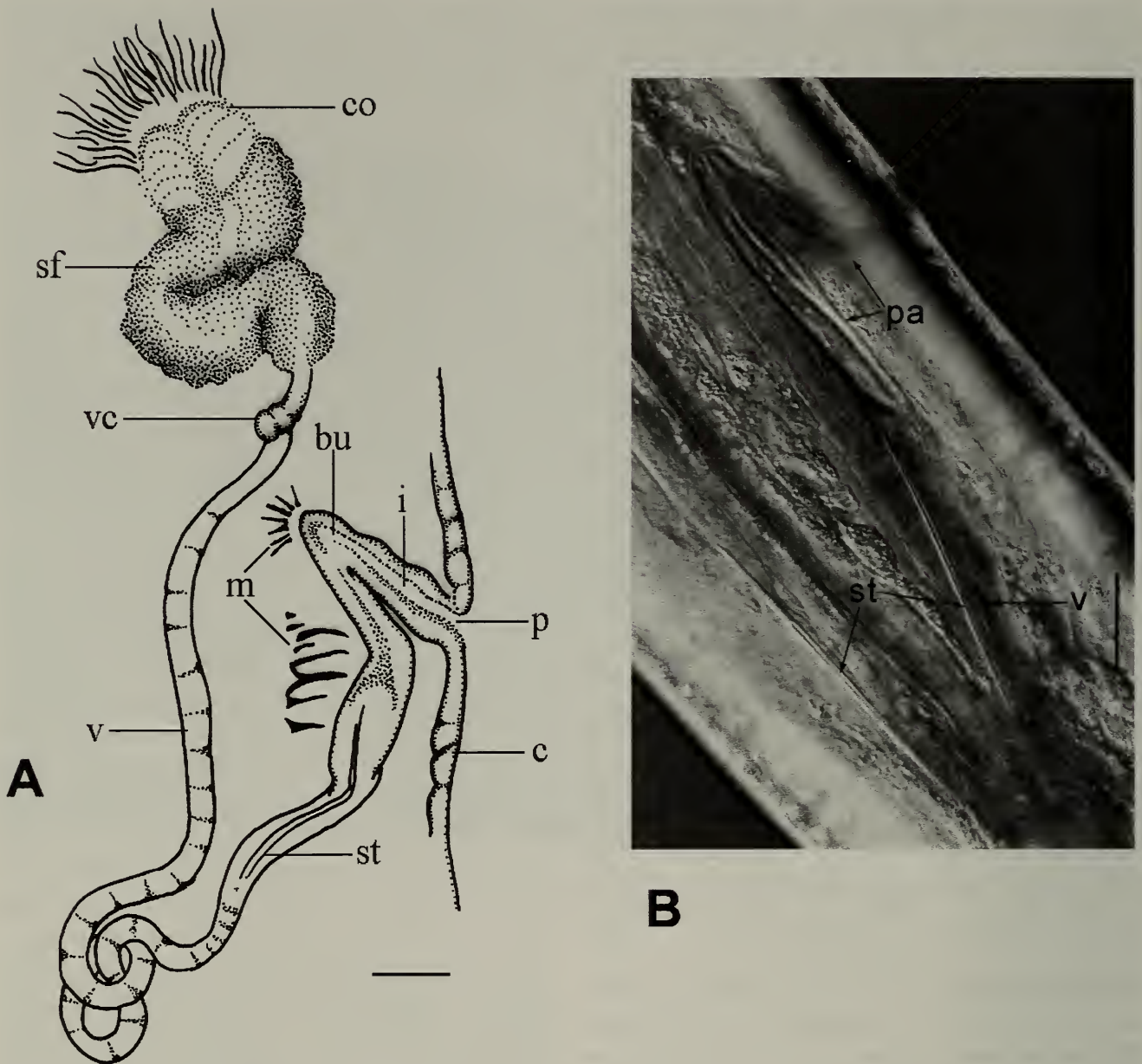


Fig. 11. *Grania hylae*, new species, from Bermuda. A, lateral view of male duct system showing sperm funnel, vas deferens and penial apparatus. B, photo of live specimen showing stylet orientation within vasa deferentia and bipartite penial apparatus. Scale equals 20  $\mu\text{m}$ . bu, union of two sections of bipartite penial apparatus; vc, vas deferens constrictions; see Figs. 2 & 5 for other symbols.

*Type material*.—Holotype USNM 53202; paratypes USNM 53203; whole mounts. Collected by P. Lasserre, 12 Nov 1973.

*Type locality*.—Castle Island, Bermuda, 32°20'40"N, 64°40'25"W. Coarse coral sand with ripple marks, 8 m depth.

*Other material examined*.—Live specimens from the southeastern tip of Paget Island, Bermuda, collected March 1998 by JML. Eleven whole mounted specimens from the collections of C. Erséus collected

from two sites in Bermuda, including the type locality (Table 1).

*Description*.—External characteristics: Length of preserved specimens 5.8–10.1 mm ( $n = 7$ ,  $\bar{X} = 7.8$ ,  $SD = 1.4$ ). Number of segments 31–59 ( $n = 7$ ,  $\bar{X} = 51.4$ ,  $SD = 9.4$ ). Diameter at 4/5 138.0–216.0  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 180.7$ ,  $SD = 27.5$ ), diameter at clitellum 159.0–258.9  $\mu\text{m}$  ( $n = 7$ ,  $\bar{X} = 217.9$ ,  $SD = 36.4$ ) (Fig. 12). Ventral setae from IV, lateral setae from XVI–XX ( $n = 7$ ). No setae in XII of mature specimens.

Ventral setae at IV–V 48.0–72.0  $\mu\text{m}$  ( $n = 14$ ,  $\bar{X} = 59.2$ ,  $SD = 7.2$ ); length of all other ventral setae 69.0–92.2  $\mu\text{m}$  ( $n = 32$ ,  $\bar{X} = 80.6$ ,  $SD = 5.9$ ); postclitellar lateral setae 75.0–96.0  $\mu\text{m}$  ( $n = 19$ ,  $\bar{X} = 83.4$ ,  $SD = 6.3$ ) (Fig. 13). In ten posterior-most segments ventral setae 68.9–74.4  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 71.5$ ,  $SD = 1.8$ ) and lateral setae 64.7–75.6  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 70.3$ ,  $SD = 3.5$ ). Setae thin with blunt proximal part possessing an upturned toe, no distinct heel present (Fig. 13). Head pore in anterior part of peristomium. Spermathecal pores paired, dorsal just posterior to 4/5, with thickened, glandular, epidermal papilla posterior to each pore (Fig. 12). Dorsal spermathecal pores about 60.0–64.4  $\mu\text{m}$  apart ( $n = 2$ ,  $\bar{X} = 62.1$ ,  $SD = 3.1$ ). Clitellum extends from posterior XI to mid XIII. Male pores ventral, in line of setae, at mid XII. Female pores slightly more lateral than male pores, just posterior to 12/13.

Internal somatic characteristics: Brain indented posteriorly. Anterior brain vesicle lacking. Pharyngeal glands present in IV–VI: with one pair of dorsolateral lobes on anterior faces of each of 4/5 through 6/7; ventrolateral lobes, one small pair in IV, two pairs in V and three pairs in VI (Fig. 12). Nephridia not observed in live specimens, however, in fixed material five to seven pairs of complete nephridia were observed in segments posterior to egg sac, about four pairs in posterior-most segments and about two to three pairs near egg sac; small overall, with small funnels. Dorsal blood vessel transition to blood sinus as far back as XX. One specimen with small gland on ventral nerve cord in XIV.

Internal reproductive characteristics: Spermathecae paired in V with narrow ental connection of ampulla to esophagus (Figs. 12 & 14). Ampulla large and round, walls very grainy, maximum diameter 42.9–106.5  $\mu\text{m}$  ( $n = 13$ ,  $\bar{X} = 80.7$ ,  $SD = 23.5$ ); sperm rings present (Fig. 14). Glands lacking at spermathecal ectal pore. Spermathecal ectal duct diameter wider closest to ampulla, diameter ranges from 10.5–19.5  $\mu\text{m}$

( $n = 12$ ,  $\bar{X} = 14.9$ ,  $SD = 3.0$ ). Ental duct runs ventrolateral to reach wall of gut, width about one half ampullar width. Sperm funnel length about four times width, non-staining, aglandular region posterior to collar (Fig. 15A). Vas deferens extending into XIII, thick and muscular along about one-third of length. Vas deferens relatively wide at sperm funnel, but lacking muscle on walls; then progressing to a short section with a spiral of muscle bands, first wound tightly around circumference of vas then unwinding so that the thick muscle bands run almost along length of the vas (Fig. 15B); muscular section followed by a thin-walled and narrow section, lacking muscle, which extends to a pad-like glandular junction with the penial apparatus (Fig. 15A, C). Maximum diameter of longitudinally muscled part is 18.0–25.5  $\mu\text{m}$  ( $n = 8$ ,  $\bar{X} = 22.9$ ,  $SD = 2.6$ ) (Fig. 15A, B), non-muscular ectal and ental vas deferens diameter 7.5–18.0  $\mu\text{m}$  ( $n = 9$ ,  $\bar{X} = 12.3$ ,  $SD = 3.2$ ). Penial stylet present, extends within ectal end of vas deferens causing that portion to be curved (Fig. 15A, C). Stylet length 91.8–130.1  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 107.9$ ,  $SD = 16.8$ ); maximum width at origin (Fig. 15C) within vas deferens 7.3  $\mu\text{m}$  (one specimen); stylet width along length 3.0–4.2  $\mu\text{m}$  ( $n = 3$ ,  $\bar{X} = 3.4$ ,  $SD = 0.7$ ). Bipartite penial apparatus consists of an erect sac-like extension from the male pore running to a lateral, anterior-posterior oriented, longitudinally ridged sac lying parallel to the body wall; stylet terminates at pore on pad in posterior, ental end of ridged sac, and can be protruded through pore and into penial apparatus (Fig. 15C). Extensions of muscles from the body wall run to the erect extension and the lateral sac, and the whole of the penial apparatus can be everted through the male pore at the body wall. Sperm sac extends to XIX. Egg sac extends to XXI.

*Taxonomic remarks.*—The only species of *Grania* recorded in Bermuda prior to this study, *G. bermudensis*, was described as a subspecies of *G. macrochaeta* by Erséus &

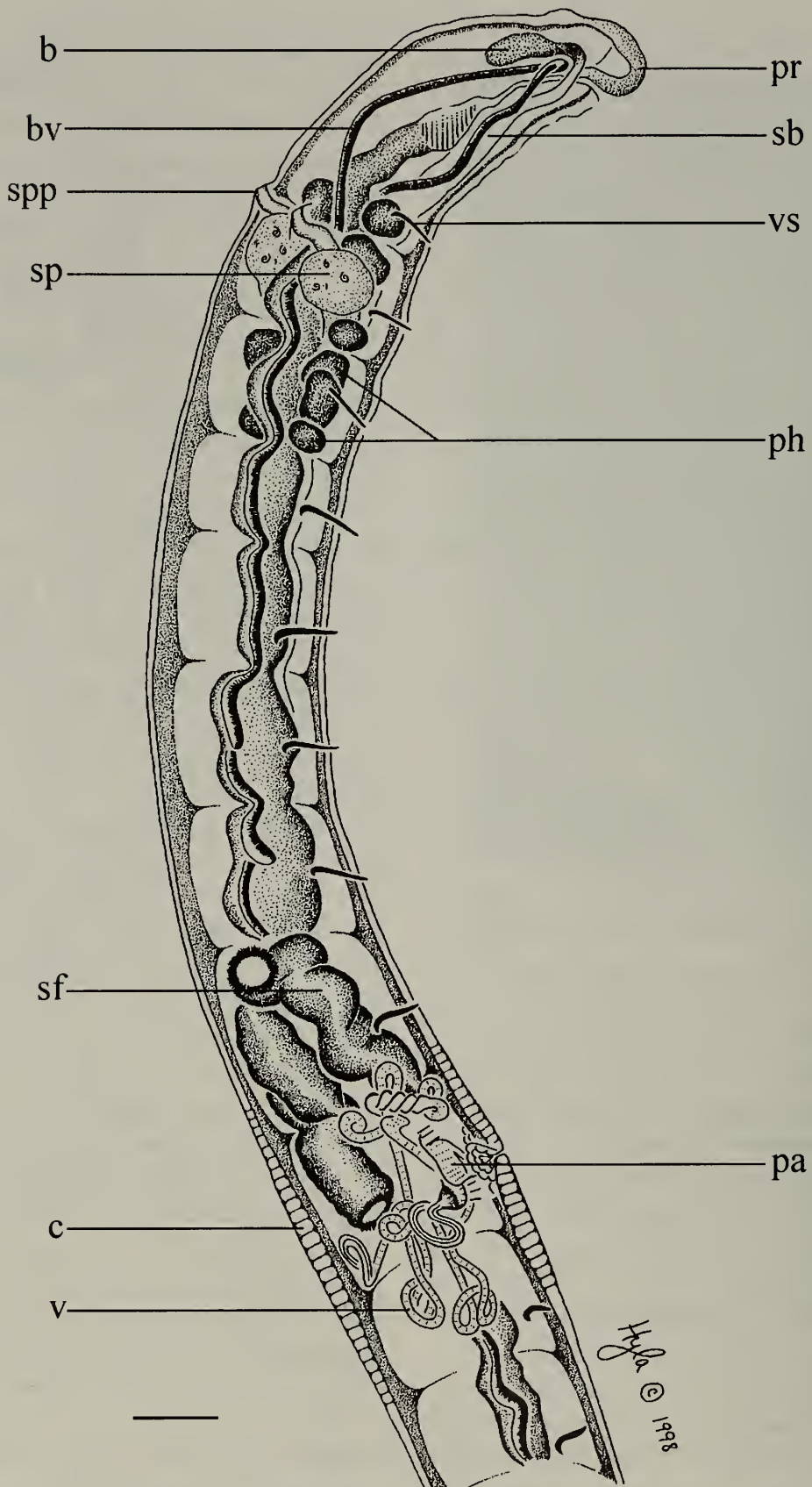


Fig. 12. *Grania bermudensis*, specimen from Bermuda. Semischematic dorsolateral view of whole mounted specimen, from prostomium to segment XIV. Scale equals 100  $\mu\text{m}$ . See Figs. 2 & 7 for symbols.

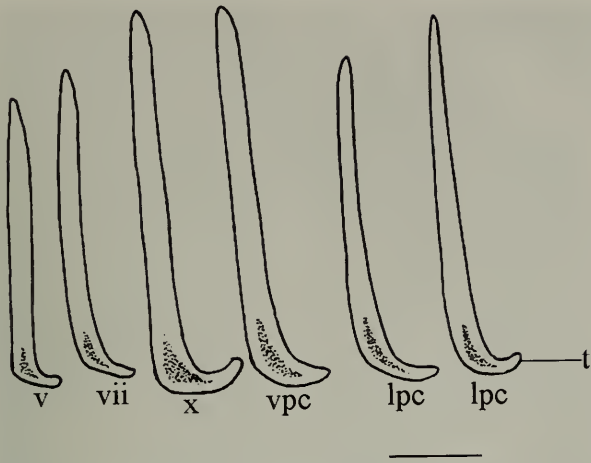


Fig. 13. *Grania bermudensis*, specimen from Bermuda. Various setae. Scale equals 20  $\mu\text{m}$ . lpc, lateral postclitellar seta; see Figs. 3 & 8 for other symbols.

Lasserre (1976). The original description of the new subspecies was brief and indefinite about some characteristics, which in part explains the classification of *G. bermudensis* within *G. macrochaeta* s. l. The group-

ing of four subspecies, *G. m. macrochaeta*, *G. m. bermudensis*, *G. m. pusilla* and *G. m. trichaeta* was recently reevaluated as taxonomically invalid based on morphological characteristics (Locke & Coates 1998) and cladistically invalid as it is polyphyletic (Locke 1999a). *Grania pusilla* has been fully redescribed (Locke & Coates 1998). This redescription of *G. bermudensis* provides details of the dorsal spermathecal pore position and male duct structures which were omitted from the original description. The distribution of lateral setae is amended from previous records of their originating in XVIII–XIX to XVI–XX.

The dorsal spermathecal pore position, bipartite penial apparatus and highly muscularized vas deferens separate this species from *G. macrochaeta* s. s. (Locke & Coates 1998) and other Bermudian congeners (Fig. 6). *Grania hylae* does share comparable modifications of the first two characters with *G. bermudensis*, however, *G. hylae*

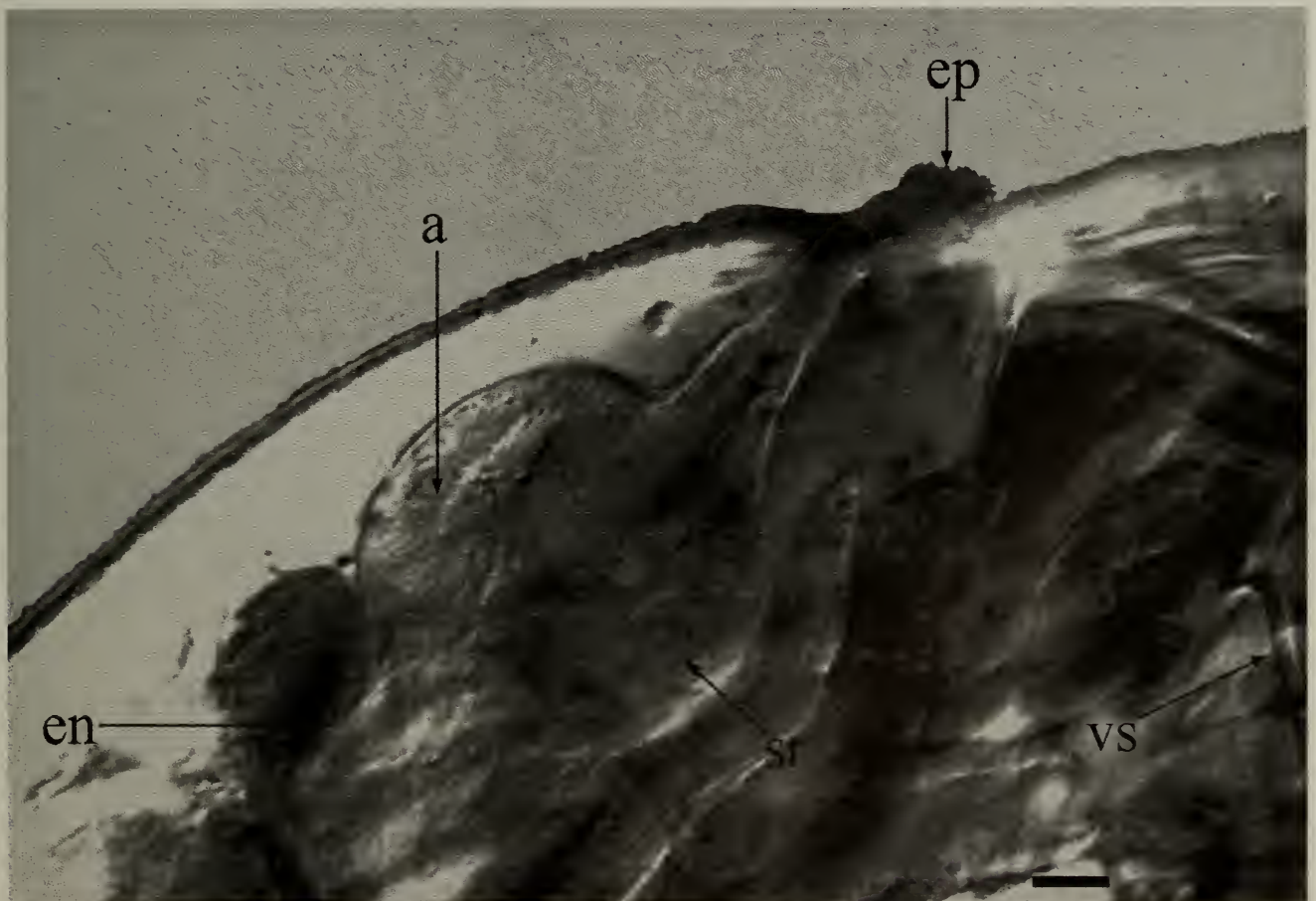


Fig. 14. *Grania bermudensis*, specimen from Bermuda. Lateral view of spermatheca with epidermal papillae. Scale equals 20  $\mu\text{m}$ . ep, epidermal papillae; see Figs. 2, 4 & 10 for other symbols.



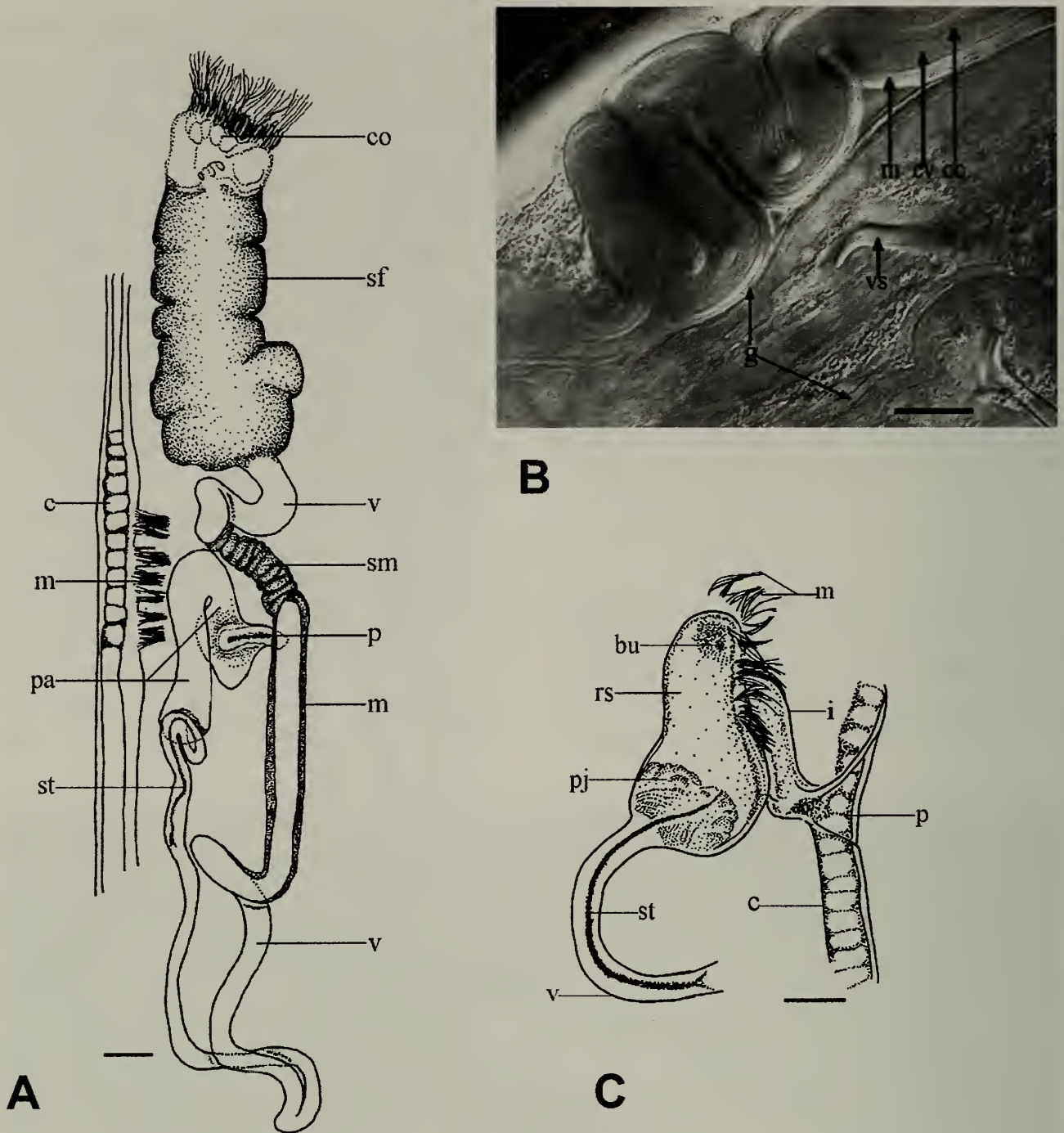


Fig. 15. *Grania bermudensis*, specimen from Bermuda. A, male duct system and penial apparatus. B, thick muscular area of vas deferens, in slightly compressed live specimen. C, lateral view of bipartite penial apparatus. Scale equals 20  $\mu$ m. bu, union of two sections of bipartite penial apparatus; cc, ciliated canal; cv, cellular vas wall; g, gut; pj, pad-like glandular junction; rs, ridged sac; sm spiral of muscle; see Figs. 2 & 5 for other symbols.

lacks the extreme muscular modifications of the vas deferens. *Grania bermudensis* is named here as a distinct species.

Other species with dorsal spermathecal pores are considered in the taxonomic remarks following the description of *G. hylae* (above) and in the Discussion.

*Habitat and distribution.*—Subtidal, medium to coarse coral sand and gravel. Not found intertidally. Found in samples with Tubificidae. Known only from Castle Island, East Castle Roads, Rushy Island, a patch reef 100 m south of Rushy Island and SE Paget Island, Bermuda (Table 1).

*Grania americana* Kennedy, 1966

Figs. 6, 16–20; Table 1

*Grania americana* Kennedy, 1966:404–405, fig 3; Erséus 1974:90–93, table 1.*Grania macrochaeta americana*: Lasserre 1967:278–280.*Grania americana* nomen dubium: Erséus & Lasserre 1976:123.

*Type material*.—Holotype, USNM 33005, paratype USNM 33039. Whole mounts. Collected by M. L. Jones 27 Aug 1962.

*Type locality*.—0.5 km from North Entrance point, West side of North Bimini, 25°43.2'N, 79°19.0'W.

*Other material examined*.—Five stained, whole mounted specimens, BAMZ 1999 180 009, Pearl Island, Bermuda; USNM 185957, Ferry Reach, Bermuda; USNM 185958 Hutchinson Island, U.S.A.; and USNM 185959 and USNM 185960, Carrie Bow Cay, Belize. About 55 live specimens from Ferry Point Bridge, Bermuda, collected by the authors over the period 1996–1998. Twenty-four whole mounted specimens from the collections of C. Erséus, collected from Bermuda; Carrie Bow Cay, Belize; Angelfish Key, Florida Keys, and Hutchinson Island, Florida (Table 1).

*Description*.—External characteristics: Live specimens notably long, with pink blood in vessels, posterior segments yellowish to light brown due to colored granules within chloragogen cells. Prostomium pointed with anterior thin region; with many multi-ciliate epidermal papillae. Fixed length 8.7–12.6 mm ( $n = 10$ ,  $\bar{X} = 10.8$ ,  $SD = 1.4$ ). Number of segments 60–74 ( $n = 9$ ,  $\bar{X} = 64$ ,  $SD = 4.8$ ). Diameter at 4/5 140.0–196.5  $\mu\text{m}$  ( $n = 15$ ,  $\bar{X} = 168.7$ ,  $SD = 18.7$ ); clitellum diameter 150.0–208.9  $\mu\text{m}$  ( $n = 15$ ,  $\bar{X} = 188.1$ ,  $SD = 19.1$ ) (Fig. 16). Setae from IV ventrally and XVI–XX laterally ( $n = 13$ ); no setae in XII of mature specimens. Setae broad at base, sometimes with slight toe and slight heel in posterior setae (Fig. 17). Anterior ventral

setae 32.6–53.3  $\mu\text{m}$  long ( $n = 10$ ,  $\bar{X} = 44.2$ ,  $SD = 8.2$ ); midbody ventrals from 53.2–60.8  $\mu\text{m}$  in length ( $n = 8$ ,  $\bar{X} = 56.3$ ,  $SD = 2.4$ ). In ten posterior-most segments ventral setae 56.6–71.3  $\mu\text{m}$  long ( $n = 21$ ,  $\bar{X} = 63.4$ ,  $SD = 3.7$ ) and lateral setae 49.2–64.1  $\mu\text{m}$  long ( $n = 16$ ,  $\bar{X} = 55.6$ ,  $SD = 4.2$ ). Head pore at anterior of peristomium. Spermathecal pores paired, lateral, posterior to 4/5 (Fig. 16). Clitellum extending over XII–XIII. Male pores in line with ventral setae, at mid XII. Female pores at 12/13, slightly more lateral than male pores.

Internal somatic characteristics: Brain indented posteriorly. Anterio-medial brain vesicle present (Figs. 16 & 18). Divided into distinct lateral halves, each containing two inclusions (for a total of four) (Fig. 18). Inclusions in each compartment located at different levels, maximum diameter of inclusions 2.5–2.8  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 2.7$ ,  $SD = 0.1$ ) (Fig. 18). Total length across both compartments of head organ 20.5  $\mu\text{m}$  (one specimen). Coelomocytes flattened and ovoid. Chloragogen cells, especially in posterior segments, very distinctive with peripherally clumped granules giving the cells the doughnut appearance of mammalian red blood cells, granules reddish-brown by transmitted light in both live and fixed specimens; outer surface of intestine, as a result, with leopard-spot pattern. Pharyngeal glands (Figs. 16 & 19) with one pair of small ventrolateral lobes in IV and a pair of dorsolateral lobes at 4/5; two pairs of ventrolateral lobes in V and a dorsolateral pair at 5/6; and with three pairs of ventrolateral lobes in VI and a dorsolateral pair at 6/7. Nephridia observed only in posterior segments, often unpaired, with small elongate funnel. Solitary, internalized, setae present in very few segments. Dorsal blood vessel transition around XXVI–XXVIII. Glands on nerve cord at XIV and/or XV.

Internal reproductive characteristics: Spermathecae (Figs. 16 & 19) paired in V with ental duct connecting ampulla to esophagus. Ampulla oviform with a maximum diameter of 42.0–90.0  $\mu\text{m}$  ( $n = 51$ ,  $\bar{X}$

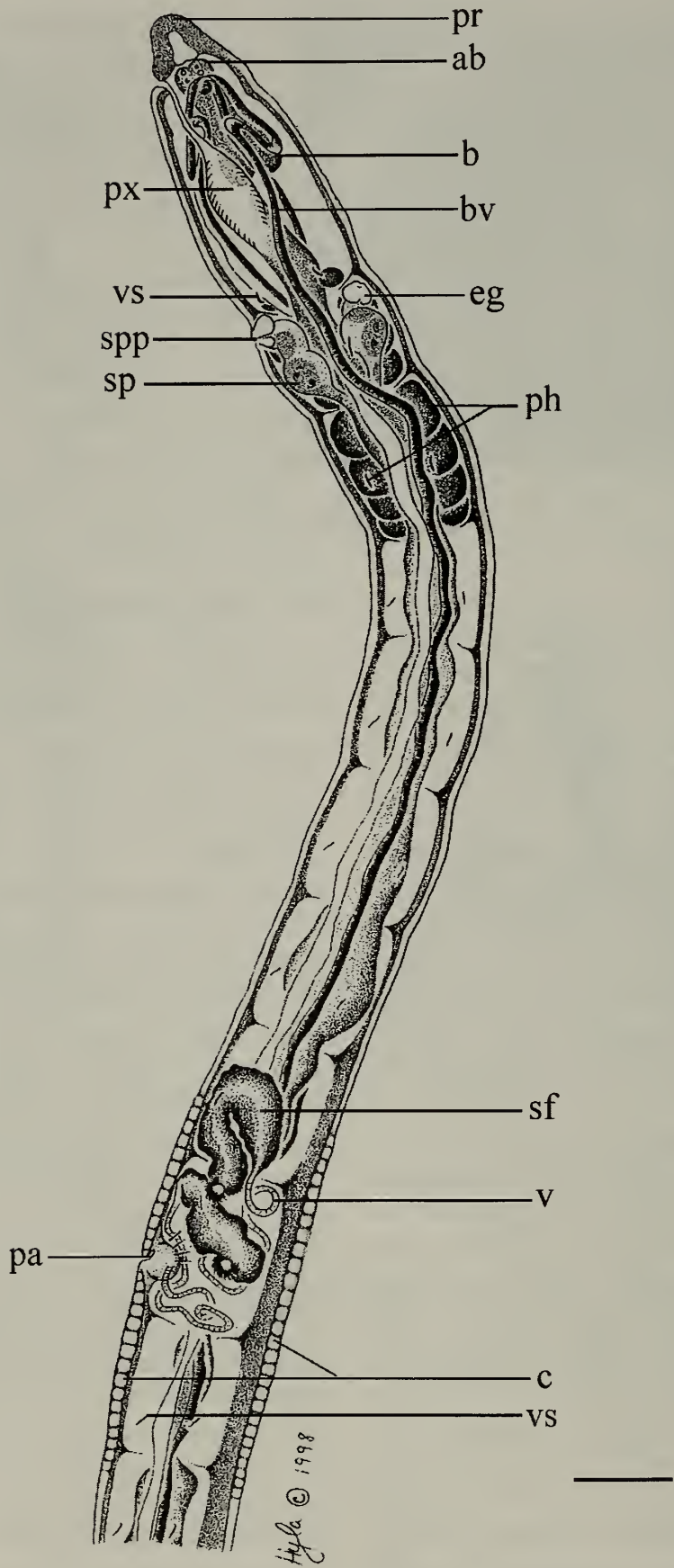


Fig. 16. *Grania americana*, specimen from Bermuda. Semischematic ventral twisted to lateral view of whole mounted specimen from prostomium to segment XIV. Scale equals 100  $\mu$ m. eg; ectal gland of spermatheca; see Figs. 2 & 9 for other symbols.

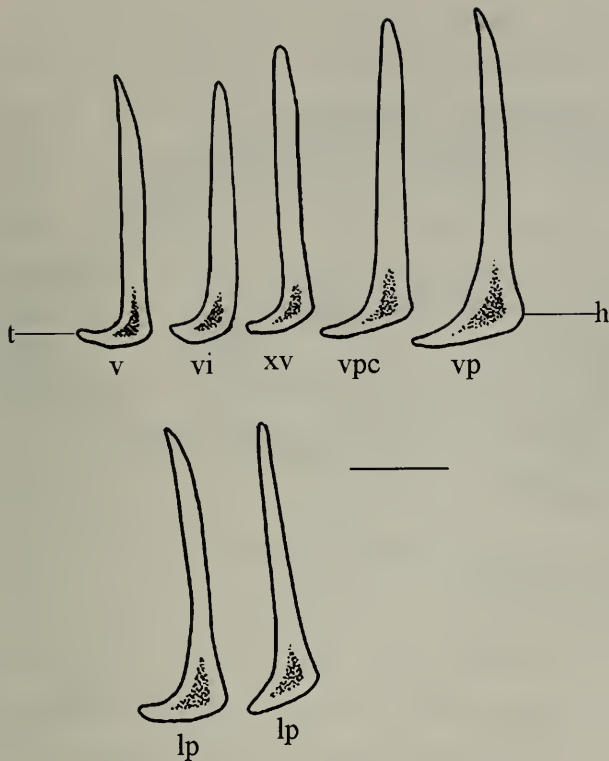


Fig. 17. *Grania americana*, specimen from Bermuda. Setae from various segments. Scale equals 20  $\mu\text{m}$ . h, setal heel; vp, ventral posterior seta; see Figs. 3 & 8 for other symbols.

= 68.5,  $SD = 11.8$ ). Spermathecal ectal duct with two glands at pore, one small and one large (Fig. 19). Ectal duct of spermatheca consists of two distinct parts: shorter part immediately adjacent to body wall with external glands and with wide canal; ental or proximal part with canal occluded by glandular cells (Fig. 19) that run as longitudinal segments around the narrow canal. Spermathecal ectal duct distal width 8.7–14.1  $\mu\text{m}$  ( $n = 6$ ,  $\bar{X} = 10.8$ ,  $SD = 2.1$ ), ectal duct medial width (max) 28.5–83.7  $\mu\text{m}$  ( $n = 8$ ,  $\bar{X} = 42.7$ ,  $SD = 17.4$ ), proximal portion of ectal duct 21.2–46.0  $\mu\text{m}$  in width ( $n = 21$ ,  $\bar{X} = 34.0$ ,  $SD = 6.7$ ). Spermathecal ectal duct length 54.0–94.7  $\mu\text{m}$  ( $n = 16$ ,  $\bar{X} = 74.3$ ,  $SD = 15.7$ ). Sperm rings present in walls of ampulla (Fig. 19). Sperm funnel length about eight times width, often displaced from XI to XII or XIII (Figs. 16 & 20A). Sperm funnel with a non-staining aglandular region immediately posterior to the collar; more posteriorly glandular tissue loose, giving funnel a very irregularly lobed surface (Fig. 20A). Sperm heads straight. Vas deferens long, extending through XIII, non-muscular, 6.8–11.4  $\mu\text{m}$  wide ( $n = 8$ ,  $\bar{X}$

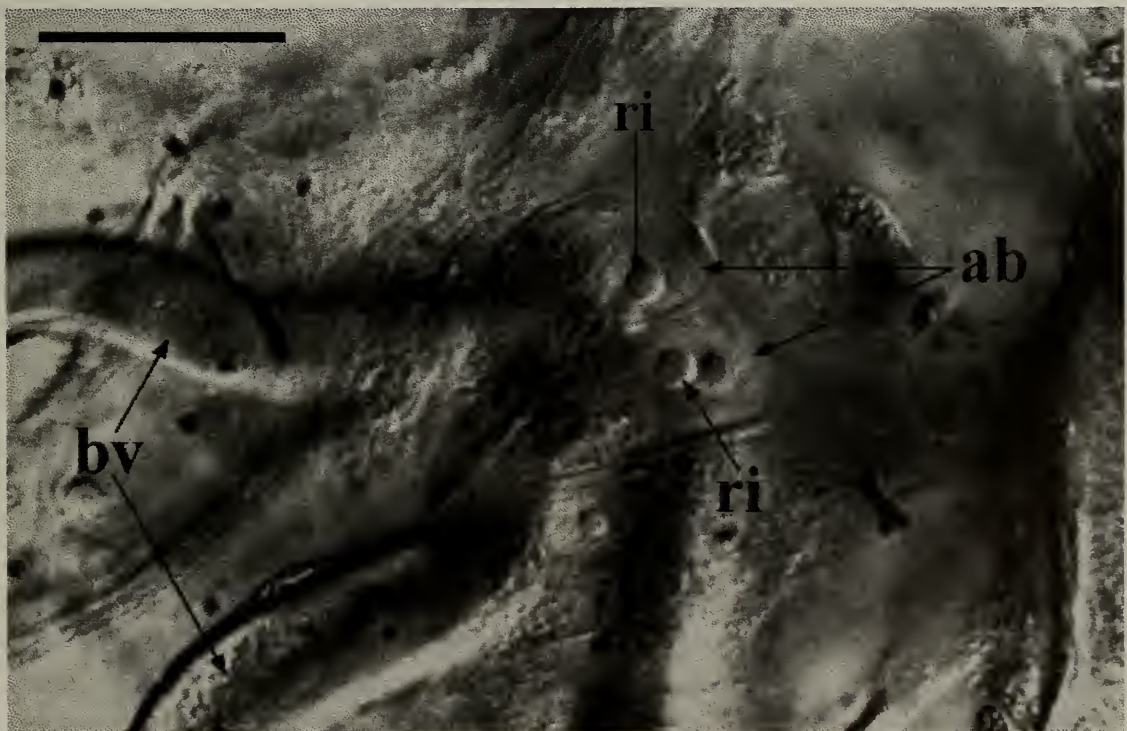


Fig. 18. *Grania americana*, specimen from Bermuda. Dorsal view of anterior brain vesicle showing inclusions. Scale equals 20  $\mu\text{m}$ . See Figs. 2 & 9 for symbols.



Fig. 19. *Grania americana*, specimen from Bermuda. Dorsolateral view of spermatheca with glands at ectal pore. Scale equals 20  $\mu$ m. See Figs. 4 & 10 for symbols.

= 9.6,  $SD = 1.7$ ). No stylet. Penial apparatus relatively simple (Figs. 16, 20A, B), with a distinct bulbous gland and an elongate, saccate dorsal extension from the male pore which extends along the lateral side of the gland (Fig. 20A, B); vas enters gland from dorsomedial side and runs to the lateral side, extending to the elongate extension. Ventrally, near epidermal pore, the penial apparatus is narrower with little glandular mass and is surrounded by very strong elaborations of the muscle bands of the body wall (Fig. 20B). Sperm sac extends to XXI. Egg sac extends to XXVII.

**Taxonomic remarks.**—Kennedy's (1966) original description of *G. americana* differs in a number of respects from our description. This is probably due to his shortage of good specimens, which limited collection of both morphometric and structural data. Kennedy did provide approximate measure-

ments for the overall length of the species (10 mm), the number of segments (50), and the ratio of length to width of the sperm funnels (several times longer than wide). However, the description was based on two specimens only. These were missing a few segments from their posterior ends and were eventually mounted in a macerating medium (pers. obs.).

The original description of *G. americana* states that the dorsal setae begin at XVI or XVIII (Kennedy 1966). In our redescription, the "dorsal" setae are described as lateral and the range of segments at which they begin is extended to XVI–XX. The presence of pharyngeal glands in VII (Kennedy 1966, Erséus 1974) was not seen in the type material when it was re-examined by us. The peptonephridia originally noted for *G. americana* have since been determined to be absent from the genus *Grania* (Erséus & Lasserre 1976) and what Kennedy observed, most likely, were the thick bundles of ducts running from the pharyngeal glands to the dorsal pharyngeal pad.

In more recent literature the taxonomic importance of the structure of the penial apparatus (Coates 1984) has become apparent, and therefore, *G. americana* which had a brief subspecies status, is not a subspecies of *G. macrochaeta* (sensu Lasserre, 1967). The penial apparatus of *G. americana* has a distinct bulbous gland, an elongate, saccate, epidermal invagination and is lacking a penial stylet. *Grania americana* also has ectal glands on the spermathecal ectal duct at the pore and these glands are visible in the type material of *G. americana*. Erséus & Lasserre (1976) had stated that these were absent in *Grania* even though they included *G. americana*. Similar glands have been noted in other recently described species (Coates & Erséus 1980, Erséus 1980, Rota & Erséus 1997) and the generic description amended accordingly.

*Grania americana* differs from other Bermudian congeners by the possession of glands at the spermathecal ectal pore, lack of penial stylet and muscular vas deferens

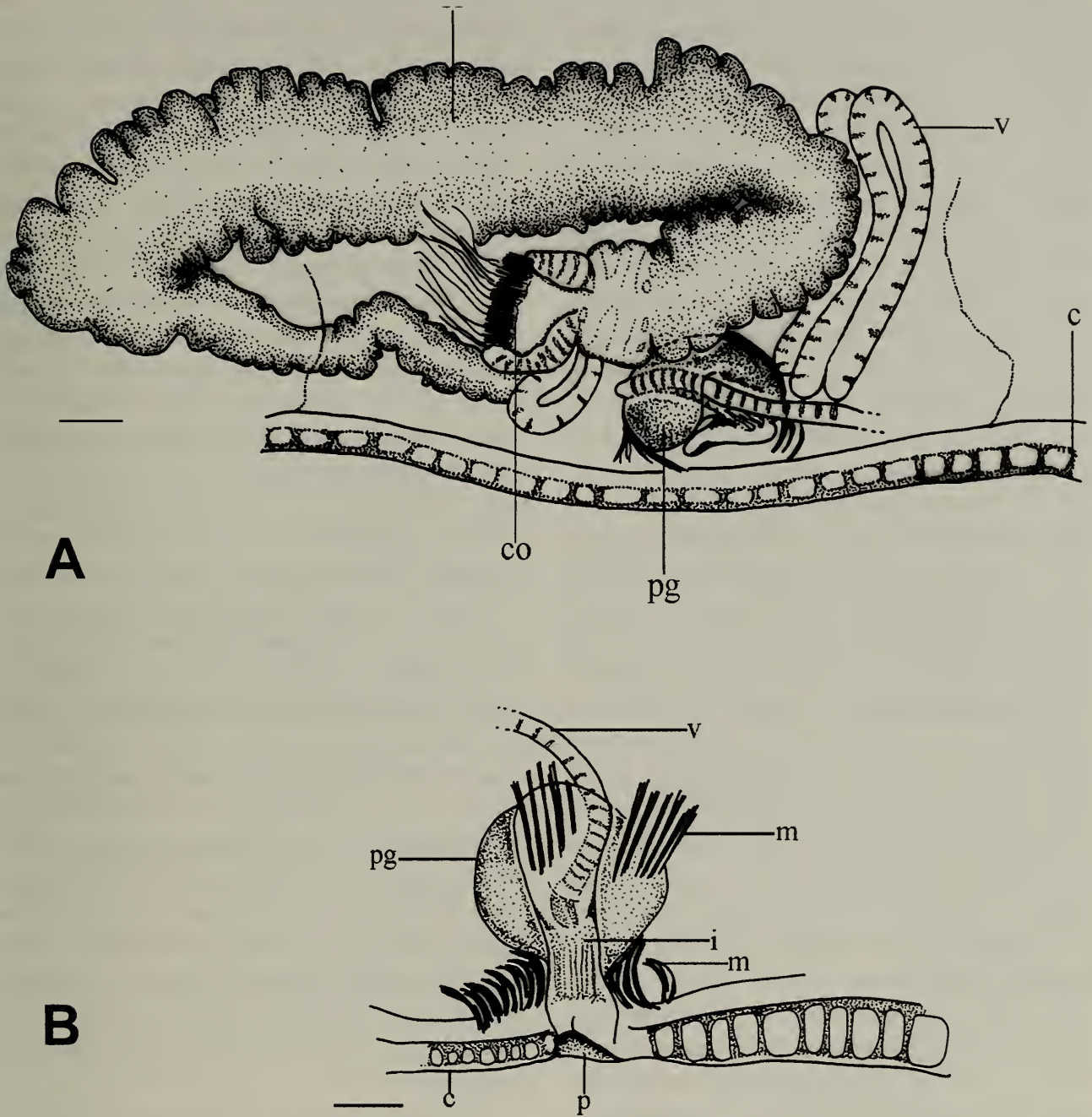


Fig. 20. *Grania americana*, specimen from Bermuda. A, dorsal view of male duct system and penial apparatus. B, lateral view of penial apparatus. Scale equals 20  $\mu$ m. See Figs. 2 & 5 for symbols.

(Fig. 6). In addition, the length of *G. americana* is much greater than that of the other species described from Bermuda. *Grania americana* possesses an anterior brain vesicle with four inclusions, described as the "head organ" in other species of *Grania* by Rota & Erséus (1996, 1997). *Grania hylae* which is also found in Bermuda has a different form of anterior brain vesicle with only one visible inclusion. In *G. americana* this organ is located in the anterior of the

peristomium, just below the boundary with the prostomium, as an anterior, medial bulbous extension of the brain. Previous accounts of this structure in recent species descriptions (Rota & Erséus 1996, 1997) have also noted the presence of four refractile bodies, but these authors (1996) also noted that some damaged specimens showed fewer inclusions or none. Quite possibly this organ has a geotactic function (Locke 1999b). A head organ has only been re-

ported for eight subtidal species of *Grania*: five from the Ross Sea, Antarctica, two from South Georgia in the subantarctic, and one from the western Atlantic. It is possible that *G. americana* shares a unique apomorphy with this subgroup of *Grania*, but is an intertidal representative of the lineage.

*Grania americana* differs from all of the other species of *Grania* which are known to have head organs by its spermathecal form, in particular large glands at the ectal pore, and distinctive ectal duct structure, penial apparatus form, and setal distribution. Two species of *Grania* are known to have single, small glands at the spermathecal ectal pore, *G. monochaeta* (Michaelsen, 1888; amended Rota & Erséus 1997) an Atlantic species and *G. paucispina* (Eisen, 1904). The first does not have a head organ with refractile inclusions, although a vesicle is present, and for the second no head organ has been described.

*Habitat and distribution.*—Coarse intertidal sand within dissolution tubes at Ferry Point Bridge and rocky limestone beach areas at Whalebone Bay, Ferry Reach, and Rocky Hill Park, Bermuda. In Bermuda also recorded from Pearl Island and Bailey's Bay in fine to medium subtidal sands. Found in samples with *G. laxartus*, various Tubificidae and Nematoda. First reported from Bimini, Bahamas; Panama City and Miami, Florida, U.S.A. Habitat at type location in Bimini was probably subtidal as Kennedy (1966) recorded that the specimens were collected "off the coast". In Florida, collected from coarse sand in *Thalassia* beds, and in shell rubble (Table 1). At Carrie Bow Cay, Belize, also found in medium to coarse sands and *Thalassia* beds (Table 1).

### Discussion

This is the first addition to our knowledge of the species diversity within *Grania* for the Northwestern Atlantic since the study by Coates & Erséus (1985). Many other species of the North Atlantic remain

to be described (pers. obs.) and further studies are required to develop an understanding of the speciation patterns and evolution of this genus. An illustrated dichotomous key to the species of *Grania* of the Northwest Atlantic can be found on the world wide web at <http://www.bbsr.edu/users/kcoates/Grania/Grania.html> (Locke 1999a).

The distributions of *Grania* species found in Bermuda pose some interesting questions about speciation and dispersal patterns, particularly because of the relatively young geological age of Bermuda, 52-34 MY. *Grania americana*, *G. laxartus* and *G. hylae* are all known from the Caribbean and Bermuda. This distribution pattern is considered typical for Bermudian fauna (Sterrer 1986, 1998). The absence of a larval stage in the development of these worms makes it difficult to explain how regular genetic exchange between Bermudian and coastal populations might be maintained. Genetic studies of Bermudian and Caribbean coastal populations could reveal information about effective "population" sizes, frequency of colonization events, and whether any existing genetic flow is unidirectional, as would seem likely due to prevailing currents. Morphological measurements for conspecific specimens from different localities did not indicate any notable differences between populations.

The intertidal pools formed within dissolution tubes at Ferry Point Bridge create an intertidal refuge for *G. laxartus* and *G. americana* which is rich in detrital matter. Healy (1996) noted the importance of crevices within the rocky intertidal as moist micro-climates during low tide. The dissolution tubes fulfill the same role as Healy's rock crevices in that they protect from wave disturbance, displacement by water currents and retain organic matter, but have high oxygen levels (Healy 1996), conditions in which enchytraeids thrive (Healy & Coates 1999). These small pots or tubes may also effectively isolate adjacent populations as the rock surface between is very exposed

and barren. This is in contrast to the subtidal habitat occupied by *G. bermudensis* and *G. hylae*. These species are protected from wave action by the greater depth of the water in which they are found and the habitat is relatively continuous. The subtidal sites in Bermuda were located to the side of major channels into bays and harbours. Tidal currents through these openings bring nutrients and detrital matter to the areas, and these get deposited in the slower water and back eddies that border the main channel.

The presence of *G. laxartus* and *G. americana* within the same samples throughout the year could conflict with commonly held ideas about ecological divergence between congeneric species. There is some evidence, other than morphological discontinuities, to suggest that co-occurring populations of the two species are biologically isolated by temporal separation of reproductive periods. High numbers of mature specimens of each species were found at different times of the year.

The muscular, bipartite penial apparatuses found in *G. bermudensis* and *G. hylae* are different from the many types of glandular, bulb-like apparatuses previously described for *Grania* species (Coates 1984). This form of penial apparatus appears to be associated with species which possess dorsal spermathecal pores. It also is found in *G. monospermatheca* which possesses a single dorsally displaced spermathecal pore. Coates (1984) had previously designated a penial bulb "Type 6" as glandular penial bulbs reduced or absent, aglandular sac often absent; with a long penial stylet plus considerable modifications to other parts of the vasa deferentia. Representative taxa were *G. bermudensis* and *G. monospermatheca*. This grouping included more structural diversity than the other "types" recognized. Additional information from the species described herein is considered and Coates (1984) "Type 6" is revised. Penial bulb "Type 6" is now described as: bipartite, saccate penial apparatus lacking a dis-

tinct glandular bulb; saccate part with horizontal and erect parts. Stylet long and contained within vasa deferentia. Muscular modifications of the vasa deferentia. Spermathecal pores dorsal. Representative taxa: *G. bermudensis*, *G. monospermatheca*, *G. hylae*, and two undescribed species from Australia (Coates 1984). Documentation of dorsal spermathecal pores and complex penial apparatuses in *G. stilifera* Erséus, 1990 and *G. inermis* Erséus, 1990 present the possibility of their being included within the Type 6 grouping. Whereas, Erséus (1990a) designated these as "Type 5" and "Type 3" (sensu Coates 1984), respectively, penial apparatuses. Other forms originally "lumped" in Type 6 await further clarification and typification.

The presence of an anterior brain vesicle in *G. americana* and *G. hylae* are the first records in readily collected species. This structure, first reported as the "head organ" by Rota & Erséus (1996), has only been found in one other species from the North Atlantic, *G. atlantica* (Rota & Erséus 1996; pers. obs). The function of the anterior brain vesicle is still unknown, but it appears to be statocyst-like in structure (Locke 1999a, 1999b). Phylogenetic studies of *Grania* species which possess this structure may provide ecological and functional hypotheses underlying the origin of such a structure in clitellates.

Although Erséus & Lasserre (1976) stated their understanding of the morphology of *Grania* had improved, they still believed that morphological differences between widely separated populations were small, sufficient only to justify their recognition as subspecies. Nonetheless, they (Erséus & Lasserre 1976:131) stated that with further studies the reinstatement of their subspecies to species could easily be made and Erséus (1977) noted that the structural variation within *G. macrochaeta* s. l. was very broad. Erséus & Lasserre (1976) also noted the importance of spermathecae in the taxonomy of enchytraeids. Locke & Coates (1998) resurrected *G. pusilla* from subspecies sta-



tus. Herein, *G. bermudensis* is recognized as even more distinct and *G. americana* is redeemed from nomen dubium (Lasserre & Erséus 1976) to full species status. The differences in spermathecal structures and in the male duct systems (Coates 1984) among these species provides sufficient support for the recognition of all the subspecies of *G. macrochaeta* as morphologically distinct species. Even more damning for *G. macrochaeta* s. l. is that this grouping of subspecies is clearly polyphyletic. Only one taxon in this group, *Grania macrochaeta trichaeata* Jamieson, 1977, awaits a full redescription.

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